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Larval and post-larval development of *Anapagurus chiroacanthus* (Lilljeborg, 1855) Anomura: Paguroidea: Paguridae

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CONTENTS

Synopsis. Four zoeal, a megalopal, first and second crab stages of the hermit crab *Anapagurus chiroacanthus* are described from laboratory reared material and compared with previous brief larval accounts of this species. Present larval evidence suggests that *A. chiroacanthus* may be phylogenetically closest to *Cestopagurus* but separated on a number of apomorphic features.

INTRODUCTION

Although our knowledge of pagurid larval development has improved considerably since Gurney's (1942) evaluation of decapod larval features, it is still relatively poor when compared with the considerable amount of information now available on brachyuran ontogeny (eg see Rice, 1980; Martin, 1984). In particular, of the 20 species currently assigned to the genus *Anapagurus,* the larval development of only six has been described (Nyblade & MacLaughlin, 1975: 286), but none of these accounts is sufficiently detailed to compare satisfactorily with the more informative larval descriptions now available of other pagurid species (Dechancé, 1961; McLaughlin & Gore, 1988).

In July 1984 two ovigerous *Anapagurus chiroacanthus* (obtained off Millport, Isle of Cumbrae, Scotland by staff of the Bryozoa Section of this Museum) were donated to the Crustacea Section. These crabs were maintained in the larval rearing laboratory until their eggs hatched. The larvae were reared through to second stage crab and provided material for the first detailed description of the complete larval and early post-larval development of this species.

MATERIALS AND METHODS

Each crab was kept in 500cm of gently aerated sea water until its eggs hatched. Larvae and the juvenile crabs were reared in plastic compartmented trays, each compartment containing 20cm of filtered water. The larvae were fed newly hatched *Artemia* nauplii and the crab stages finely shreaded macerated *Littorina* tissue; all were maintained at 12–15°C. Small lengths of plastic conduit were provided and eventually accepted by juvenile crabs as a shelter. Development time, from hatching to the appearance of second stage crab, took an average of 82 days.

All material was initially fixed and stored in the solution formulated by Steedman (1976: 148) and was later transferred to 70% industrial methylated spirit.

Dissected appendages were transferred to glycerol as temporary micro-slide preparations, and drawings were made using a *camera lucida* attached to an Olympus BH2–NIC microscope. Setal types were identified using interference contrast (Nomarski) and confirmed by viewing with a Hiatachi S800 field emission scanning electron microscope.

The crabs and reared material are deposited in the Collection of the Zoology Department, British Museum (Natural History), accession number: 1989: 191.

Measurements: (average measurements of 4–5 specimens) C.L. = carapace length measured from tip of rostrum to median posterior margin of carapace for larval stages. S.L. = shield length measured from rostral apex to shield posterior margin, for crab stages, T.T. = total length measured from rostral apex to posterior margin of telson.

RESULTS

Anapagurus chiroacanthus (Lilljeborg, 1855)

Larval references. *Spiropagurus chiroacanthus:* Sars, 1890:155, Tab. 3 (prezoea, zoea, I, IV, megal); *Anapagurus chiroacanthus*: MacDonald et al, 1957:243, fig. 10 (zoeae I–IV, megal); Pike & Williamson, 1959:3, figs 34–38, 53

(zoeae I–IV, megal); Pike & Williamson, 1960:525, fig 8E (zoea I).

Zoea I.

C.L. 1.0mm., T.L. 2.10mm.

CARAPACE (Fig. 1a). Longitudinally strongly convex in lateral view. Rostrum stout reaching well beyond apex of antennule exopod and slightly more than half median length of carapace; posterio-lateral spine stout.

EYES. Well developed and partly fused to carapace.

ABDOMEN (Figs. 1a, 2a, b, 17a). 5-segmented, segment 5 longest. Posterio-dorsal margins of 1–3 with 4 (sometimes 5 on 3) minute denticles; 4,5 each with pair of stout spines. Posterio-lateral margins of 2,3 each with 2 denticles; 4,5 each with spine and sometimes pair of small lateral simple setae.

TELSON (Figs. 2a, 16a). Slightly broader than long, measured from base of short cuspidate/spiniform* furcal setae. Posterior margin convex with single row of large denticulettes and armed with 5 plumodenticulate setae on each half and an outermost small pappose seta; second innermost plumodenticulate seta longest and fifth shortest.

ANTENNULE (Fig. 1b). Exopod sub-cylindrical, with 1 subterminal plumose seta, 2 short and 1 long terminal aesthetasc.

ANTENNA (Figs. 1c, 17b). Protopod with stout denticulate medio-distal spine. Exopod broad (maximum width about half length), with long denticulate stout disto-external spine measuring about half exopod length; exopod with 9 marginal plumose setae (innermost short and stout) and 1 simple seta next to disto-external spine. Endopod shorter than exopod (maximum width about one quarter of length), narrowing slightly distally and with 2 terminal plumose setae.

MANDIBLES (Fig. 1d). Well developed, incisor differentiated from molar process, both mandibles of similar shape.

MAXILLULE (Fig. 1e). Exopod 3-segmented, terminal segment longest, with 1,1,2 plumodenticulate setae, short on segment 1. Basis distally narrowed, terminating as 2 stout equally developed cuspidate setae with sockets hardly discernible and bearing 4–7 graded denticles. Coxa broad, distal margin with 5 long thin plumodenticulate setae, 2 short sub-marginal simple setae and a few short disto-internal microtrichia.

MAXILLA (Figs. 1f, 18a). Scaphognathite lobe developed anteriorly only and with 5 short marginal plumose setae. Endopod 'stepped' ie with broad outer and much smaller inner lobe bearing 3,3 plumodenticulate setae. Basis bilobed, each with small distal process and 4,4 setae (3 plumodenticulate and one innermost simple on each lobe), outer margin of endite with few microtrichia. Coxa bilobed with 2,7 plumodenticulate setae, inner margin of endite with few microtrichia.

MAXILLIPED 1 (Figs. 2c, 18b, c). Basis with 1–1–3–3 plumodenticulate setae on inner margin. Endopod 5-segmented with 3,2,1,2,4+1 plumodenticulate setae, all except last arising from inner distal margins; outer distal margins of segments 2–4 with microtrichia; setules investing plumodenticulate setae on segment 5 varying from hardly discernible to stout and long (see pl. 3c). Exopod incipiently divided medially and with 4 long distal plumose setae.

MAXILLIPED 2 (Fig. 2d). Basis with 1 stout plumodenticulate and 1 simple seta on inner distal margin. Endopod 4-segmented, with 2,2,2,4+1 setae; setae on inner margins of segments 2–4 represented by at least two distinct plumodenticulate types (see inset to figure); microtrichia on outer margins of segments 2,3. Exopod incipiently divided medially and with 4 distal long plumose setae.

MAXILLIPED 3 (Fig. 2e). With incipiently developed basis and exopod.

Zoea II

C.L. 1.25mm., T.T. 2.55mm.

CARAPACE (Figs. 3a). Rostrum distally slightly curved downwards and usually not longer than half median length of carapace.

ABDOMEN (Fig. 3a, 4b, c). Posterio-dorsal margin of segment 3 with 6 (sometimes more) minute denticles. Posterio-lateral margins of segments 2,3 usually with only one small posterior denticle.

TELSON (Figs. 3k, 4a). Posterior margin with an additional innermost pair of small plumodenticulate setae (total of 7 plumodenticulate setae on each half).

EYES (Fig. 3b). Free from carapace margin; cornea very broad.

ANTENNULE (Fig. 3c). Exopod with one long stout aesthetasc and 4 thin shorter ones.

ANTENNA (Figs. 3d, 17c). Protopod with a disto-external spine. Exopod narrower (maximum width much less than half length), with 10 plumose setae; most posterior seta on inner margin of exopod much longer than in previous stage and seta next to disto-external spine plumose. Endopod basally broadened.

MANDIBLES (Fig. 3e). Molar processes relatively broadened and less noticeably differentiated from incisor portions.

MAXILULLE (Figs. 3f, g). Basis (f) with 2 additional slightly smaller spiniform setae (grading to cuspidate type) and in some specimens a minute marginal simple seta. Coxa (g) with innermost plumodenticulate seta stout.

MAXILLA (Fig. 3h–j). Scaphognathite (j) with 6–7 marginal plumose setae. Basis (h) with one additional plumodenticulate seta on inner lobe (total of 4,5). Coxa (i) with one additional ?simple seta on outer lobe (total of 3,7).

MAXILLIPED 1 (Fig. 4d). Endopod segments 1–3 each with one long plumose seta on disto-outer margin; microtrichia absent. Exopod with 7 distal plumose setae.

MAXILLIPED 2 (Fig. 4e). Endopod segments 2,3 each with one long plumose seta on disto-outer margin; microtrichia absent. Exopod with 7 distal plumose setae.

MAXILLIPED 3 (Fig. 4f). Articulation between basis and exopod incomplete. Exopod incipiently divided medially, distally with 6 plumose setae.

PLEOPODS (Fig. 4a). Posterior-ventral part of segment 6 with very incipient plepod buds.

* Some specimens have small denticles on surfaces of these setae thus placing them into the cuspidate category. See p. 00 for terminology.

Zoea III

C.L. 1.4mm., T.T. 3.10mm.

CARAPACE (Fig. 4g). Rostrum much shorter than median carapace length.

ABDOMEN (Fig. 5a–c). Sixth segment developed. Posterio-dorsal margin of segment 1 variably denticulate or unarmed. Segments 2,3 with 4–5 denticles. Segments 4,5 with additional pair of small denticles. Segment 6 unarmed. Posterio-lateral margins of segments 2,3 variably denticulate as shown in b.

TELSON (Fig. 5a, d). Dorsal surface with pair of small simple setae. Furcal and plumodenticulate setae on posterior margin slightly shorter than in previous stage; second innermost plumodenticulate seta replaced by stout spine, denticulate in distal half.

ANTENNULE (Fig. 5e). Peduncle incipiently 2-segmented; small disto-external simple seta present and more or less medially placed longer plumodenticulate seta. Exopod with 6 aesthetascs. Endopod developed as conspicuous bud partly sutured from peduncle and with one proximal plumodenticulate seta, one apically placed plumose seta and one aesthetasc.

ANTENNA (Fig. 5f). Endopod distally acute and with only one (?)simple sub-distal seta present.

MANDIBLES (Fig. 4h). Incisor region broader and with a more complex dentition.

MAXILLULE. Setation and shape unchanged.

MAXILLA (Fig. 5g). Scaphognathite with 9 marginal plumose setae; setation of other endites unchanged.

MAXILLIPED 1. Setation of endites unchanged.

MAXILLIPED 3. (Fig. 5h). Exopod with 7 plumose setae. Endopod present as conspicuous bud almost as long as basis.

PEREIOPODS (Fig. 4g). 1–4 developed as incipient buds.

PLEOPODS (Fig. 5a). Exopod of uropod well developed, almost as long as telson, thin, tapering distally into acute process invested with small denticulettes, inner margin with 6 long plumose setae.

Zoea IV

C.L. 1.82mm., T.T. 3.85mm.

CARAPACE (Fig. 6a). Posterio-lateral spine much smaller than in previous stages.

ABDOMEN (Fig. 7a–c). Posterior-dorsal margins of segments variably denticulate but segment 5 usually with additional pair of small denticles. Segments 1–5 each with a pair of dorso-median simple setae. Denticulation of posterio-lateral margins variable but segments 5, 6 always with small but prominent posterio-ventral spine.

TELSON (Fig. 7d). Posteriorly narrower. Innermost pair of plumodenticulate setae on posterior margin generally shorter than in previous stages. Dorsal surface with 2 pairs of median simple setae.

ANTENNULE (Fig. 6b). Peduncle usually with 2 disto-external simple setae. Exopod now with 9 aesthetascs, 2 strongly sub-distally placed.

ANTENNA. Endopod equal in length or slightly longer than exopod, otherwise unchanged.

MANDIBLE (Fig. 6c). Dentition of left mandible noticeably different from right mandible.

MAXILLULE (Fig. 6d, 17d). Coxa with 2 additional plumodenticulate setae, otherwise setation unchanged.

MAXILLA (Fig. 6e, f). Scaphognathite posterior lobe developed and bearing 3 terminal, one sub-terminal and 13 anteriorly placed plumose setae (total 16 setae). Some coxal setae on inner lobe noticeably stouter than in previous stages.

MAXILLIPEDS 1, 2 (Fig. 6a). Exopods with 8 plumose setae, otherwise unchanged.

MAXILLIPED 3 (Fig. 6a). Endopod longer than in previous stage.

PEREIOPODS (Fig. 6a). 1–4 rudimentary. Pereiopod 1 (cheliped) incipiently segmented and with dactyl differentiated from distal propodus. 2 & 3 also incipiently segmented.

PLEOPODS (Fig. 7a, d, e). Developed as paired buds on segments 2, 3 (=pairs 1, 2). Pleopod 5 (uropod), exopod dorsal surface with 2–3 simple setae and with one additional distally placed simple seta on inner margin (total of 7 marginal setae). Endopod represented as a small bud bearing a distal plumose seta.

Megalopa

C.L. 1.0mm., T.T. 2.10mm.

CARAPACE (Fig. 8a, 9a). Longer than broad and subquadrate from dorsal aspect. A well developed sub-acute rostrum present. Anterior margin on either side slightly convex. Ocular acicles spinose. Surface of carapace sparsely setose at most.

ABDOMEN (Fig. 9a, 11d, e, 19a, b). Six-segmented. Segment 5 longest; margins of segments unarmed. Surfaces of segments 1, 4–5 with one, and of segment 6 with two pairs of dorsal simple setae in addition to pappose lateral setae present (as shown in Fig. 11d & 19a, b). Posterio-lateral margins of segments sub-truncate to rounded).

TELSON (Fig. 11d, 19d). Sub-oval to sub-quadrate, as broad as long or, where lateral margins are inflated (as in some specimens), slightly broader than long. Dorsal surface with 2 pairs of simple setae and one lateral pair present. Posterior margin with 8 long plumose setae.

EYES (Fig. 8a). Much longer than broad, reaching into basal segments of antenna.

ANTENNULE (Fig. 9b). Peduncle 3-segmented. Segments 1, 2 subequal. Segment 3 long and distally expanded. Outer surface of segment 1 with an oblique row of 6–7 plumose setae, lower margin with a distal lobe bearing one simple and one plumodenticulate seta, dorsal margin with 2 plumodenticulate and one simple seta (see inset to figure). Segment 2 with 2 distal simple setae. Segment 3 with 2 ventral and one dorsal simple seta. Exopod incipiently 4-segmented; only segment 4 usually clearly differentiated. Segments 2–3 respectively with a ventral group of 5 aesthetascs, 2 aesthetascs and a dorsal simple seta. Segment 4 with a proximal group of 3 aesthetascs, 4 terminal simple setae and a small spiniform seta (see inset to figure). Endopod 2-segmented; segment 1 with 2 and segment 2 with 6 setae (2 sub-distal).

ANTENNA (Fig. 9c). Peduncle 5-segmented. Segment 2 with 2 simple setae, distal inner margin armed with one stout spine and outer with 2 spines, one of which is ventrally placed. Segment 3 sub-triangular and with one simple seta. Supernumerary segment not visible. Segment 4 much shorter than 5 and with one simple seta. Segment 5 with 4 distal setae. Acicle (exopod) armed with 6 simple setae and terminating in 2 acute processes. Flagellum 10-segmented; segment 1 shortest; setal formula 0, 4, 1–2, 6, 1, 5, 0, 5, 3, 7–8.

MANDIBLES (Fig. 9d). Molar and incisor processes differentiated into two oval-shaped slightly concave structures without teeth or spines. Palp large, 3-segmented and with 1–2 small simple setae on distal part of segment 3.

MAXILLULE (Fig. 9e, f, 19c). Exopod reduced to simple lobe. Setae on basis reduced in size but increased in number and represented by 10–11 spiniform setae (fig. 19c) and 2 stout short plumodenticulate setae. Coxal setae reduced in number to 2–3 stout plumodenticulate and one simple seta.

MAXILLA (Fig. 8b–d). Scaphognathite with well developed anterior and posterior lobes and with 25 marginal plumose seta. Endopod reduced to simple lobe with one sub-apical simple seta. Basis with 8, 7 setae, many setules and denticles now reduced or absent, conveying appearance of simple setae (c). Coxa with 3, 3 plumodenticulate setae.

MAXILLIPED 1 (Fig. 8e). Coxa hardly demarcated from basis and with plumodenticulate and simple seta. Basis with small proximal spiniform seta and 4–5 simple setae on inner margin. Endopod as elongated lobe. Exopod developed as incipiently 2-segmented non-setosed lobe.

MAXILLIPED 2 (Fig. 8, f). Protopod elongated. Endopod developed as 2-segmented non-setosed lobe. Exopod 2-segmented, apex of segment 2 with 6 plumose setae.

MAXILLIPED 3 (Fig. 10a, 20a). Endopod with ischium to dactyl developed. Ischium with one plumodenticulate seta on disto-inner margin and merus with one on disto-outer margin. Carpus with transverse row of 6 plumodenticulate setae near distal margin. Propodus with 13–20 setae chiefly near inner and distal margins represented by small cuspidate and two types of plumodenticulate setae. Dactyl with 6–8 setae composed of two plumodenticulate types (p1, p2 in Fig. 20a). Exopod 2-segmented, apical part of segment 2 with 8 plumose setae.

PEREIOPODS 1 (CHELIPEDS) (Fig. 10b–e). Left cheliped (b, c) all segments clearly differentiated. Merus long, longitudinally sub-triangular and with one distal spine on both inner and outer margins. Carpus short, sub-triangular and with 3 spines on outer margin. Propodus and dactyl slightly compressed. Upper margin of propodal prolongation with number of spines, as shown in inset to (c). Lower margin of dactyl with at least 5 spiniform setae. Cheliped segments invested with simple and plumodenticulate setae disposed as shown in figures. Right cheliped (d, e), merus sub-triangular, with small spine on upper distal inner margin. Carpus sub-triangular with 2 small spines on upper margin. Propodus and dactyl somewhat compressed. Upper margin of propodal palm with 2 small spines, lower with several small irregular teeth or spines. Upper margin of propodal prolongation and lower margin of dactyl somewhat cristate and bearing several iregularly shaped teeth as shown in inset to (e). Cheliped segments with plumodenticulate and some simple setae (e, d).

PEREIOPOD 2 (Fig. 10f, 20b, c). Long and relatively stout, all segments clearly differentiated. Length of ischium slightly less than half length of merus. Dactyl almost as long as combined lengths of propodus and carpus. Merus and propodus with a conspicuous spine on lower distal margin. Ischium to propodus invested only with simple setae. Dactyl with simple and pappose setae (Fig. 20b, c).

PEREIOPOD 3 (Fig. 11a). Long and relatively stout; all segments clearly differentiated. Ischium greater than half length of merus. Dactyl almost as long as combined lengths of propodus and carpus. Upper distal margin of carpus and lower distal margin of propodus with spine. Ischium to propodus invested only with simple setae. Dactyl with simple and pappose setae.

PEREIOPOD 4 (Fig. 11b). Short and robust; all segments differentiated. Propodal outer surface with 5 pseudochaetal type setae. Segments invested with only plumodenticulate setae distributed as shown.

PEREIOPOD 5 (Fig. 11c, 20d). Short and robust; all segments clearly differentiated. Propodal distal outer surface with *circa* 8 pseudochaetal type setae and one on dactyl. Segments invested with plumodenticulate setae of various lengths.

PLEOPODS (Fig. 11d, e, f–j). Only pleopods 1–3 and 5 fully developed. Pleopods 4 represented as pair of buds. Pleopods 1, 2 with long protopod (h, i). Exopod short, bearing 8 long plumose setae. Endopod small, with two distal cincinnuli on inner distal margins. Pleopod 3 (j) exopod with 4 distal plumose setae; endopod absent. Outer margins of protopod and exopod with microtrichia. Pleopods 5 (uropods) of equal size. Exopod with *circa* 9 pseudochaetal type setae on outer distal part, 10 plumose and 5 plumodenticulate setae. Endopod small, with 3 pseudochaetal type setae, one proximal simple and one distal plumodenticulate seta.

GILLS (Fig. 12a). Origin of gills difficult to resolve, but at least 6 on each side in megalopa; all appear to be arthrobranchs.

Crab I

Shield length 0.56mm.

CARAPACE (Fig. 12b). Anterior margin of shield convex. Lateral projections obtuse. Ocular acicles swollen medially and distally acute. Ocular extension broad.

ABDOMEN (Fig. 15a). Segmentation indistinct and with slight increase in numbers of setae.

TELSON (Fig. 15a, d). Subquadrate. Posterior margin strongly concave, irregularly dentate and with one pair of simple setae. Dorsal surface with 5 pairs of simple setae.

EYES (Fig. 12b). Length slightly more than maximum width (measured from base of peduncle).

ANTENNULE (Fig. 12c). Peduncle 3-segmented. Segment 3 not distally expanded. Outer surface of segment 1 with oblique row of 7 or more plumose setae, lower margin with broad distal lobe bearing plumose seta and well developed spine. Segment 2 shortest. Segment 3 with 2 dorsal plumose setae but still with 2 ventrally placed simple setae. Exopod 5-segmented with 0, 6, 5, 3 aesthetascs on segments 1–4 and 3 simple distal setae on segment 5. Endopod unchanged but distal spiniform seta on segment 2 no longer present.

ANTENNA (Fig. 12b, e). Peduncle now 6-segmented. Segment 1 with 3 very small plumose setae on inner margin and a small spine on outer margin. Segment 2 with 7 simple setae, outer distal margin with the more dorsally placed distal spine reduced to an obtuse process. Segment 3 with one distal simple seta but with dorsally placed innermost distal obtuse process. Supernumary segment visible and intercalated below base of acicle. Apex of acicle terminating as acute process armed with average of 5 simple setae. Flagellum with 11 segments and a setal formula of 0, 0, 3, 2, 5, 1, 5, 1, 6, 4, 7–8.

MANDIBLES (Fig. 12f). Molar part differentiated as a transverse obtuse lobe. Incisor part forming broad slightly concave plate-like expansion. Outer distal part of protopod with prominent simple seta. Segment 1 of palp indistinctly sutured from protopod. Segment 3 with 8 cuspidate setae and one plumodenticulate type on distal margin.

MAXILLULE (Fig. 12g). Protopod with outer stout plumodenticulate seta without or with very few setules; outer margin of protopod with a lamellar expansion bearing marginal microtrichia. Exopod with long simple seta on inner apical margin. Basis with average of 13 cuspidate and 2 stout plumodenticulate seta (total of 15, see inset to figure). Coxa with total of 16 setae, at least 10 cuspidate type and others plumodenticulate, some probably grading from one form to the other (see figure inset).

MAXILLA (Fig. 13a). Scaphognathite with average of 20 marginal plumose setae, 5 posterior setae still noticeably separated from others. Sub-apical seta on endopod represented as plumose type. Basis with 10, 10 plumodenticulate setae, many with setules and denticles very reduced or absent (see uppermost inset). Coxal outer lobe with 6 marginal and one submarginal plumodenticulate seta; inner lobe with 7 marginal plumodenticulate and a row of 13 sub-marginal plumose setae, proximal margin also with microtrichia.

MAXILLIPED 1 (Fig. 13b, c). Coxa differentiated from basis with average of 5–7 plumodenticulate setae. Basis with 20 setae, cuspidate grading into plumodenticulate, as shown in (c). Endopod with one plumodenticulate seta. Exopod well developed, clearly 2-segmented, one outer proximal plumose seta and one inner medial simple seta on segment 1; distal margin of segment 2 with 6 plumose setae.

MAXILLIPED 2 (Fig. 13d, 14a). Endopod developed and segments clearly differentiated, except basis/ischium. Coxa expanded and with 6 setae. Basis with 3 setae on inner margin. Ischium with 2, merus and carpus one, propodus 6 and dactyl with 5 setae, all plumodenticulate types (Fig. 14a). Exopod long and thin. Segment 1 with outer medial simple seta. Segment 2 still with 6 terminal plumose setae.

MAXILLIPED 3 (Fig. 14b). Endopod-ischium with 6 plumodenticulate setae on or near inner margin and a distal cuspidate seta. *Crista dentata* developed and composed of 5 spines; accessory tooth incipient. Merus to dactyl with setae; average setal counts respectively 5, 5, 16, 9 for these segments, of plumodenticulate type (see inset). Exopod segment 1 with 2 simple setae and one plumodenticulate seta. Segment 2 with average of 7 plumose setae.

PEREIOPODS 1 (Fig. 14c, d). Left cheliped (d) general proportions and spine investment unchanged except for upper margin of propodal prolongation and lower margin of dactyl, both with numerous spiniform setae. Right cheliped (c), propodal palm broad, upper and lower margins noticeably convex. Upper margin of propodal prolongation and lower dactyl margin cut into broad irregular teeth and with spiniform setae disposed as shown in inset to figure.

PEREIOPODS 2, 3. Unchanged except for slight changes in relative lengths of some segments and their setation.

PEREIOPOD 4 (Fig. 14e). Unchanged except for shape and slight increase in number of pseudochaetae on propodus.

PEREIOPOD 5. Unchanged except for slight increase in number of propodal pseudochaetae.

PLEOPODS (Fig. 14g, f, 15a–c). Pleopod 4 (g) developed. Pleopods without endopod. Numbers of plumose setae on exopod segment 2 slightly variable. Average of 8 on 1–3 and 5 on 4. Pleopod 5 (uropods), left (b) larger than right (c). Plumose setae on exopods of uropods virtually absent; numbers of pseudochaetae increased by one or 2 at most.

Crab II

Shield length 0.60mm.

CARAPACE. Anterior margin now with small lateral projections similar to adult.

ANTENNULE. Peduncular segment 1 outer surface with average of 14 obliquely placed plumose setae. Flagellum with few additional aesthetascs. Endopod 3-segmented.

ANTENNA. Peduncular segments unchanged. Flagellum with some additional segments.

MANDIBLE. Molar part distinct and whole mandible similar in shape to adult.

MAXILLULE. Basis and coxa with many additional setae; ventral surfaces with row of setae developed similar to adult although fewer in number.

MAXILLA. Scaphognathite with average of 25 plumose marginal setae. Endopod distally tapering into thin process, similar in shape to adult. Many additional setae on basis and coxa.

MAXILLIPED 1. Setal numbers increased and plumodenticulate setae present on lower surface of basis. Exopod segment 1 longer than in previous stage.

MAXILLIPED 2. Merus relatively longer than in previous stage (proportionally similar to adult). Setal numbers on propodus and dactyl increased and similar to adult.

MAXILLIPED 3 (Fig. 15g). Setal numbers increased on all endites. *Crista dentata* now well developed and with 11–12 obtuse spines, accessory tooth well developed.

PEREIOPODS 1 (Fig. 15e, f). Left cheliped (f), carpus proportionally longer than in previous stage and with 3 prominent spines on outer margin. Upper margin of propodal prolongation and lower margin of dactyl with fewer setae. Right cheliped (e), carpus with 3 robust spines on upper margin. Upper and lower margins of propodal palm cristate and dentate.

PEREIOPOD 3. Dactyl lower margin with one spiniform setae.

PEREIOPOD 4. Propodus with average of 13 and dactyl with 8 pseudochaetae.

PLEOPODS. Left pleopod 1 very reduced in two specimens available for study; 2–4 well developed and still uniramous.

Pleopods on right side of abdomen absent. Pleopod 5 (uropod), left noticeably larger than right. Exopod with average of 17 and of right 13 pseudochaetae arranged in two rows. Endopod with 5 pseudochaetae.

REMARKS

Larval morphology of the genus *Anapagurus* is poorly known when compared with other pagurid genera. Of the twenty species attributed to *Anapagurus* (see Gordan, 1956) the larval stages of only six are known and the complete larval development has been only briefly described for five of these species (see Sars, 1890; MacDonald *et al.* 1957; Pike & Williamson, 1960; Dechancé, 1961; Dechancé & Forest, 1962).

The first and fourth zoea and the megalopa of *A. chiroacanthus* was described by Sars (1890) from Norwegian plankton-collected material and brief accounts were given of the complete larval development by MacDonald *et al.* (1957) and Pike & Williamson (1959) and of the first stage zoea by Pike & Williamson (1960). These descriptions were based on laboratory hatched first zoeas and reared plankton-collected stages from Plymouth, Port Erin, the Irish Sea, Firth of Clyde and Naples.

The present reared material originating from the Millport region of the Firth of Clyde differs from previous larval accounts of *A. chiroacanthus* in the features listed below.

Sars (1890) gives the length of zoea I as '1½mm' (*cf.* 2.10mm average length of Millport material) and shows: *telson* posterior margin with longest pair of setae proportionally longer than in Millport material; *antennule* with 4 aesthetascs (*cf.* 3 in Millport material); *mandibles* incisor process much less prominent; *maxillule* exopod with 0, 1, 3 setae (*cf.* 1, 1, 2), coxa with 6 setae (*cf.* 7); *maxilla* endopod 3, 2 setae (*cf.* 3, 3), coxa 3, 7 setae (*cf.* 2, 7); *maxilliped* 1 basis with 1–2–2 setae (*cf.* 1–1–3–3 setae), endopod segments 1–4 each with an outer marginal distal seta and with 1, 2, 1, 2 inner marginal setae (*cf.* segments 1–4 with outer distal marginal microtrichia and 3, 2, 1, 2 setae on inner margin); *maxilliped* 2 basis with 1 distal inner marginal seta (*cf.* 2), endopod segment 3 with 1 outer marginal seta (*cf.* without a seta but with microtrichia).

Zoea IV, *antennule* with a transverse suture demarcating basis from endopod and exopod buds, 6 or 7 aesthetascs/setae and 1 plumose seta (*cf.* without a suture in Millport material, 2 plumose setae and 9 aesthetascs); *antenna* endopod bud incipiently segmented, peduncle ?without a small outermost spine (*cf.* without segmentation and with a small outermost peduncular spine); *maxillule* basis with 1–2 submarginal setae (*cf.* without submarginal setae), coxa with 6 setae (*cf.* 9); *maxilla* scaphognathite with 10 anterior and no posterior setae (*cf.* 14 anterior, one medial and 3 posterior setae) endopod with 3, 2 setae, basis 4, 4, coxa 4, 6 (*cf.* 3,3 4,5 3,7 setae on respective endites); *maxillipeds* exopods of 1, 2, 3 with 5, 6, 5 setae respectively (*cf.* 8, 8, 7 setae); *pereiopod* 5 developed (*cf.* indistinct); *pleopods* exopod of uropod with 6 setae (*cf.* 7 setae).

Megalopa, '2½mm' (*cf.* average 2.10mm); *rostrum* obtusely oval (*cf.* sub-acute in Millport specimens); *pereiopods* cheliped propodus noticeably broadened (*cf.* only moderately broadened), pereiopod 3 dactyl sub-equal to propodus (*cf.* much longer than propodus), pereiopod 4 dactyl only slightly longer than propodus (*cf.* much longer than propodus); *pleopods* developed on segment ?5 (*cf.* not present on segment 5); *telson* longer than broad and with 12 marginal plumose setae (*cf.* about as long as broad and with 8 setae).

MacDonald *et al.* (1957) and Pike & Williamson (1959) show; zoea I, *telson* posterior margin with longest pair of setae (ie 2nd plumodenticulate pair) longer than in Millport material.

Zoea II, *telson* 4th seta on posterior margin (ie 3rd plumodenticulate) slightly shorter than 5th (ie. 4th plumodenticulate) (*cf.* slightly longer in Millport specimens).

Zoea III, *uropods* extending into posterior 4th of telson (*cf.* posterior 7th); *telson* 3rd seta (ie 2nd plumodenticulate developed as spine) on posterior margin relatively much longer than in Millport material, setae on telson dorsal surface ?absent (*cf.* one pair present).

Zoea IV, *pleopods* present on segments 2–4, 6 (*cf.* on 2, 3, 6 in Millport material); uropod with 6 exopod setae (*cf.* 7); *telson* 3rd seta (ie 2nd plumodenticulate seta developed as spine) on posterior margin much broader than in Millport material, dorsal surface of telson ?without setae (*cf.* 2 pairs).

Megalopa, *rostrum* figured as obtuse and described as 'very blunt' (*cf.* subacute in Millport specimens); (*cf.* 12); *pereiopods* cheliped propodus noticeably broadened (less broad in Millport specimens); *pleopods* uropod with 10–12 exopod setae (*cf.* average 15); *telson* longer than broad and ?without dorsal setae (*cf.* almost as broad as long and with 2 pairs of setae).

The present laboratory reared material of *Anapagurus chiroacanthus* enables comparisons to be made between the megalopa, early juvenile and adult stages. The following morphological features are shared by the megalopal and first stage crab. *Antennule*; peduncular segment 1 with oblique ridge of setae on outer surface and disto-dorsal setae on peduncular segment 3, endopod 2-segmented. *Antenna*: the same number of flagellum segments and setation. *Maxilla*: distal seta on endopod and posteriorly narrowed scaphognathite. *Pereiopod* 2: subapical spine on meral lower margin, propodal distal spine on lower margin and similar overall setation of segments. *Pereiopod* 3: spine on carpal upper distal margin and propodal distal spine on lower margin. *Pereiopod* 5: similar overall setation of propodus and dactyl. *Telson*: 2 pairs of setae on dorsal surface.

The following features of *A. chiroacanthus* are common to the first stage crab and the adult. *Antennule*: peduncular segment 1 with oblique ridge of setae* on outer surface and subdistal spine and distal obtuse process on lower margin. *Antenna*: peduncular segment 2 with outer dorso-lateral process and developed supernumary segment. *Mandible*: with small but prominent seta on protopod. *Maxillule*: with propodal lobe and distal seta on endopod. *Maxilla*: with prominent sub-distal row of plumose coxal setae. *Maxilliped* 2: segment 2 of exopod with single outer marginal seta, basis with only 6 setae. *Maxilliped* 3: segment 2 of exopod with outer mid-point seta, accessory tooth developed on ischium of endopod. *Pereiopod* 2: lower margin of merus with subapical spine* and propodal distal spine.* *Pereiopod* 3: spine on upper distal carpal* margin and on lower distal propodal* margin.

* Also present in megalopal stage.

Fig. 1 *Anapagurus chiroacathus* ZOEA I: **a** whole larva from left lateral aspect; **b** left antennule; **c** left antenna (upper inset shows details of spine & lower inset the simple seta on this margin); **d** mandibles from ventral aspect; **e** left maxillule; **f** left maxilla. (Scales **a** = 100μm, others 50μm).

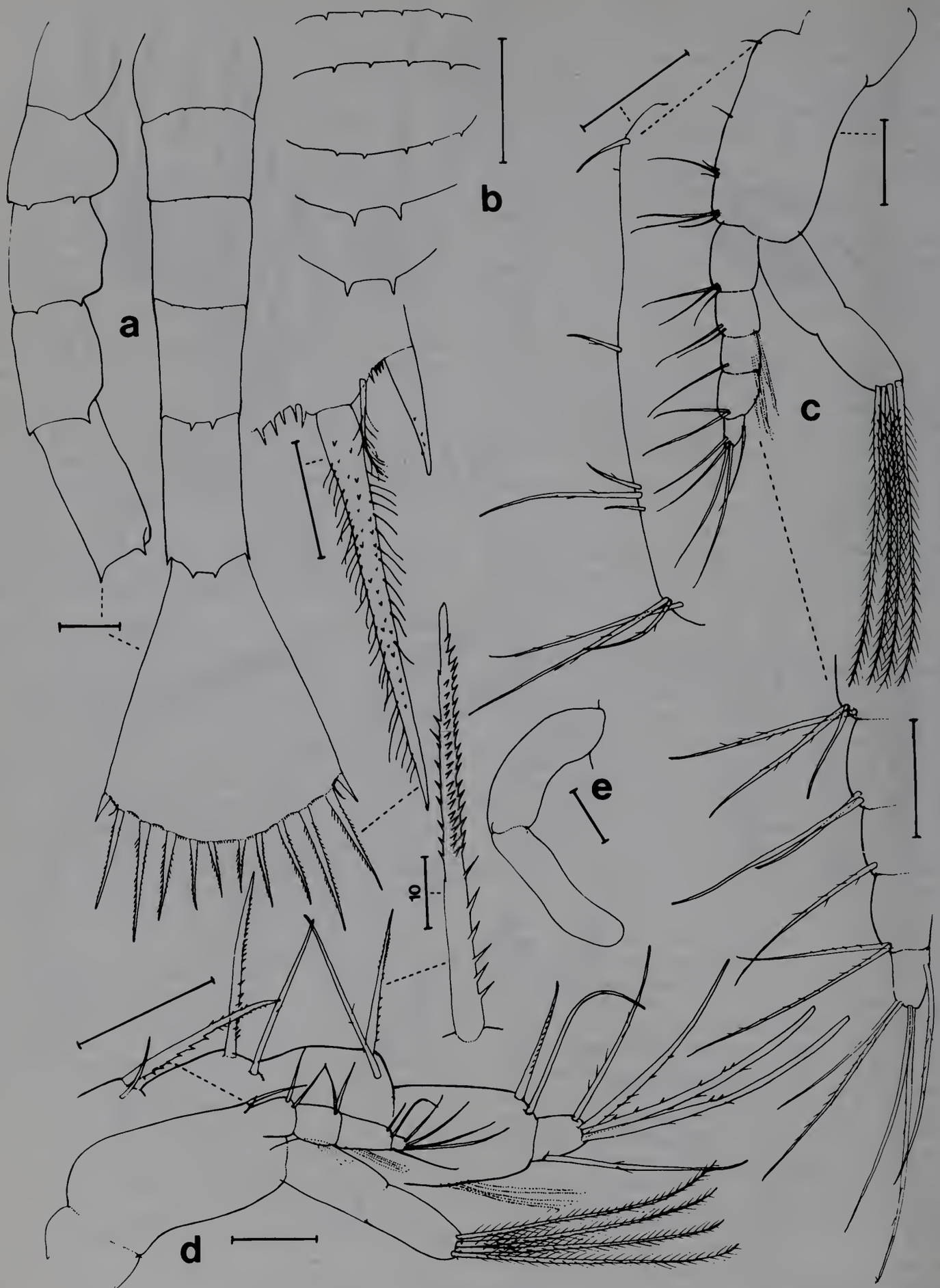

Fig. 2 *Anapagurus chiroacanthus* ZOEA I: **a** abdomen and telson, dorsal (right) and lateral (left) aspects; **b** posterio-dorsal margins of abdominal segments 1–5; **c–e** maxillipeds 1–3 from left side. (Scales **a–c** = 100μm, **e** & inset = 50μm, except where indicated).

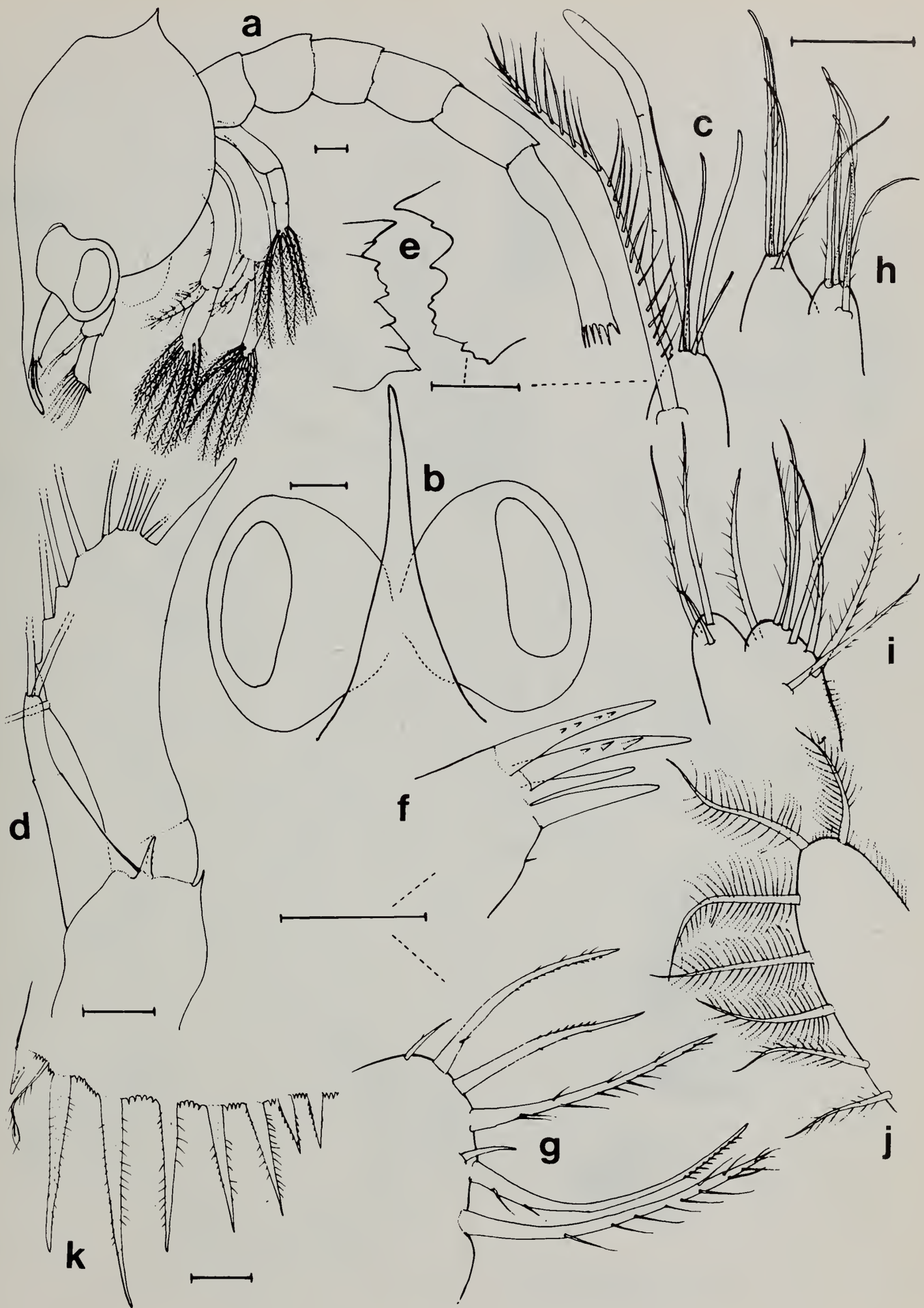

Fig. 3 *Anapagurus chiroacanthus* ZOEA II: **a** whole larva from left lateral aspect; **b** dorsal view of eyes and rostrum; **c** distal part of left antennule; **d** left antenna; **e** incisor and molar parts of mandibles; **f, g** distal parts of basis and coxa of right maxillule; **h, i, j** basis, coxa and scaphognathite of right maxilla; **k** left posterior margin of telson. (Scales **a, b** = 100μm, others = 50μm).

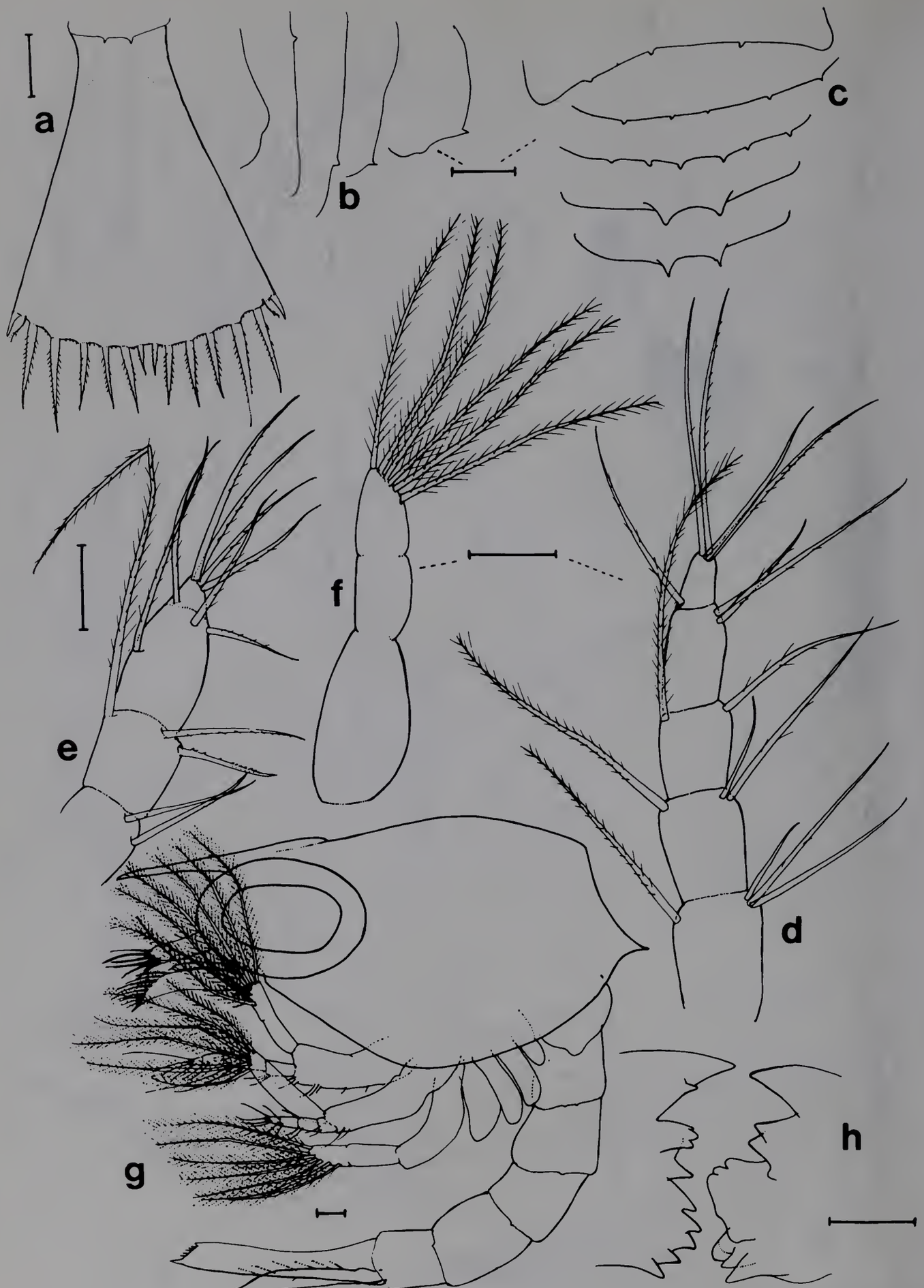

Fig. 4 *Anapagurus chiroacanthus* ZOEA II: **a** telson in dorsal aspect; **b** posterio-lateral and **c** posterio-dorsal margins of abdominal segments 1–5; **d** endopod of right maxilliped 1 and **e** of maxilliped 2; **f** right maxilliped 3. ZOEA III **g** whole larva from left lateral aspect; **h** mandibles from ventral aspect. (Scales **a**, **g** = 100μm, others = 50μm).

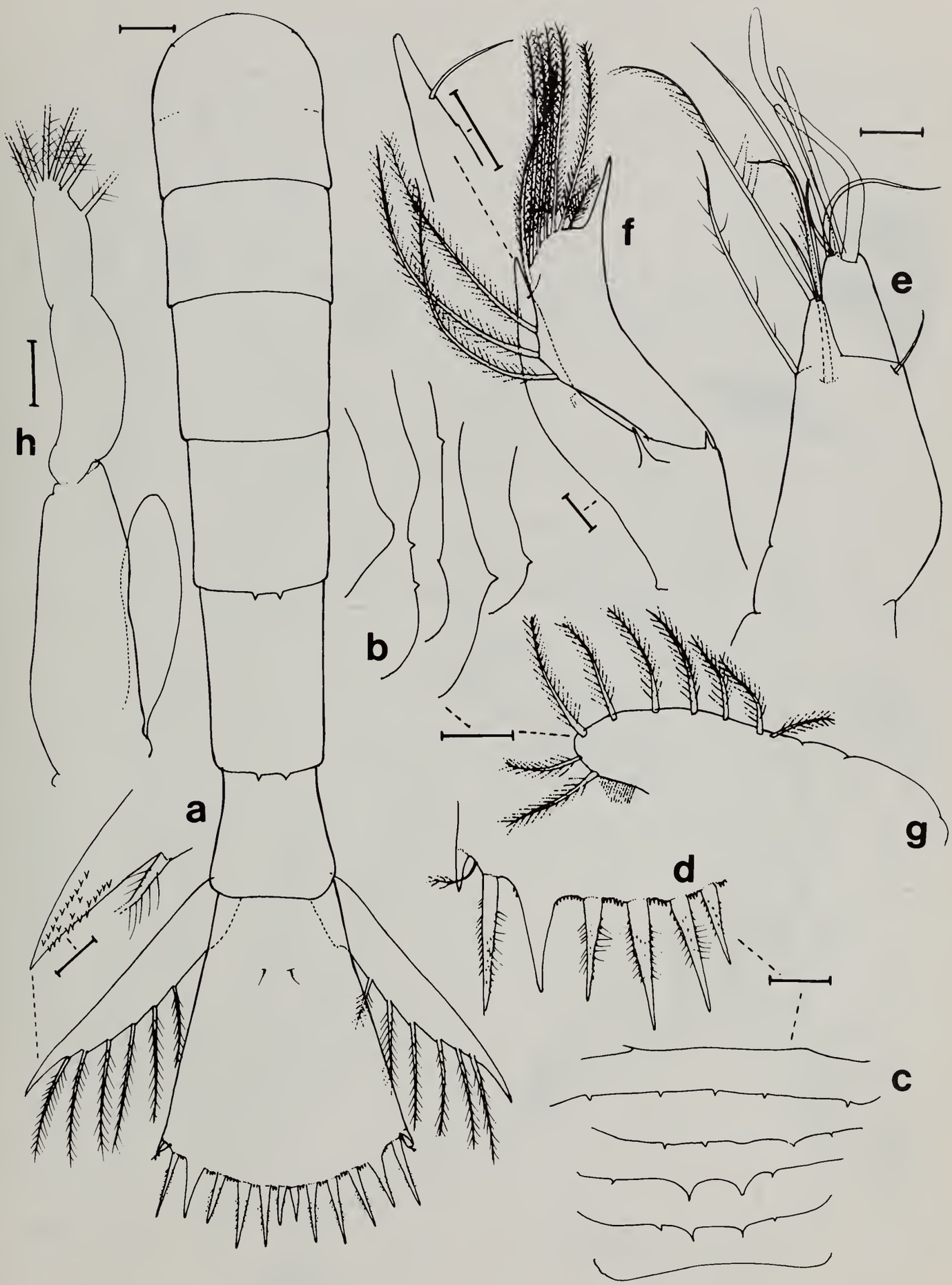

Fig. 5 *Anapagurus chiroacanthus* ZOEA I: **a** abdomen, telson and uropods from dorsal aspect; **b** posterio-lateral margin of abdominal segments 1–5; **c** posterio-dorsal margins of abdominal segments 1–6; **d** left half of telson posterior margin; **e** right antennule; **f** right antenna; **g** scaphognathite of left maxilla; **h** left maxilliped 3. (Scales = 100μm, others = 50μm, except inset to **a** = 20μm).

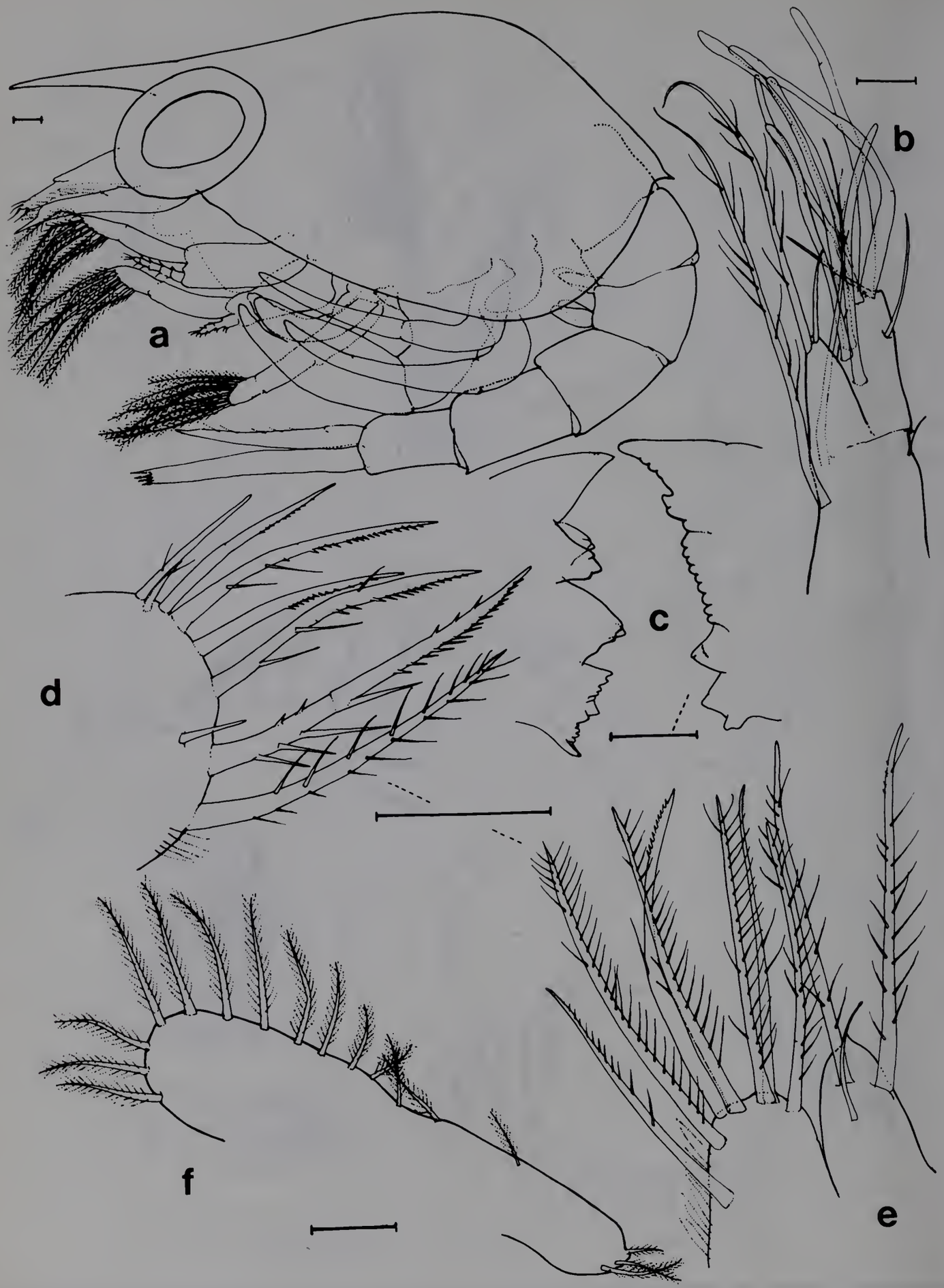

Fig. 6 *Anapagurus chiroacanthus* ZOEA IV: **a** whole larva from left lateral aspect; **b** right antennule; **c** mandibles from ventral aspect; **d** right maxillule coxa; **e** left maxilla coxa; **f** left maxilla scaphognathite. (Scales **a** = 100μm, **b, c, f** = 50μm, **d, e** = 30μm).

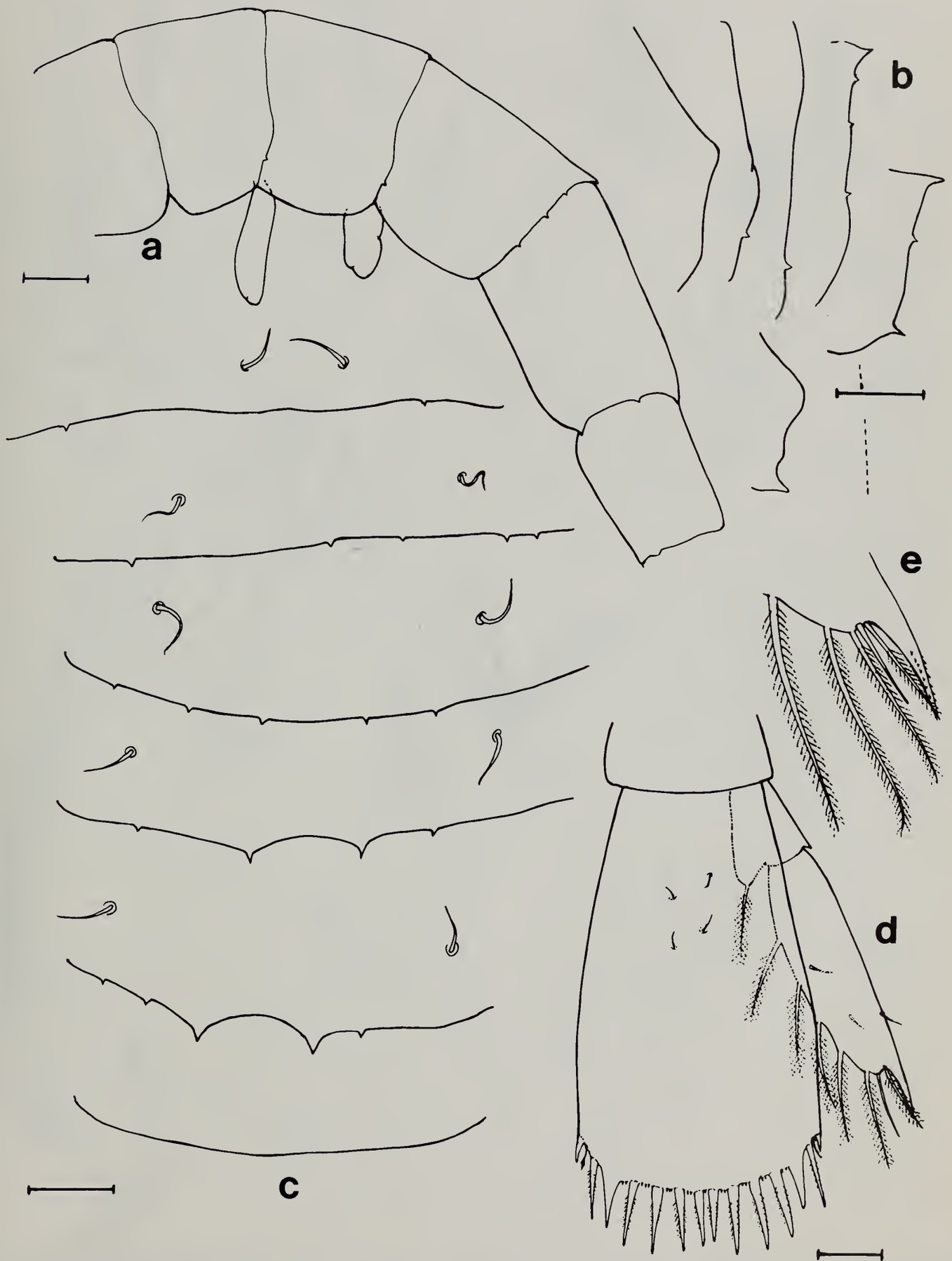

Fig. 7 *Anapagurus chiroacanthus* ZOEA IV: **a** abdominal segments 1–6 from left lateral aspect; **b** posterio-lateral margins and **c** posterio-dorsal margins of abdominal segments 1–6; **d** telson and right uropod from dorsal aspect; **e** distal part of uropod. (Scales 50μm, except **c** = 30μm).

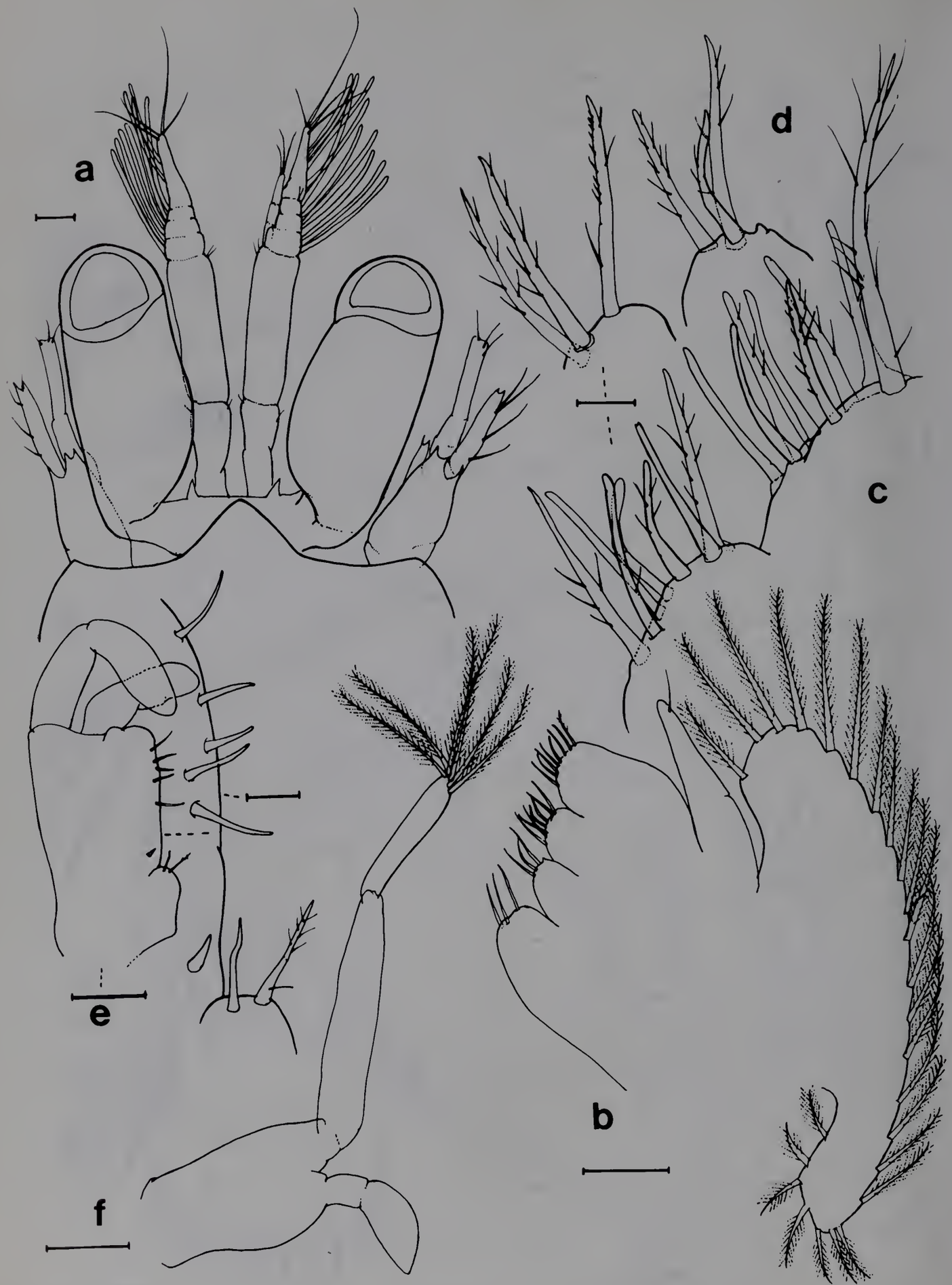

Fig. 8 *Anapagurus chiroacanthus* MEGALOPA: **a** dorsal aspect of anterior part of body; **b** right maxilla; **c, d** basis and coxa of maxilla; **e, f** right maxilliped 1 & 2. (Scales **a–c, f** = 50μm, **e** = 100μm, inset = 20μm).

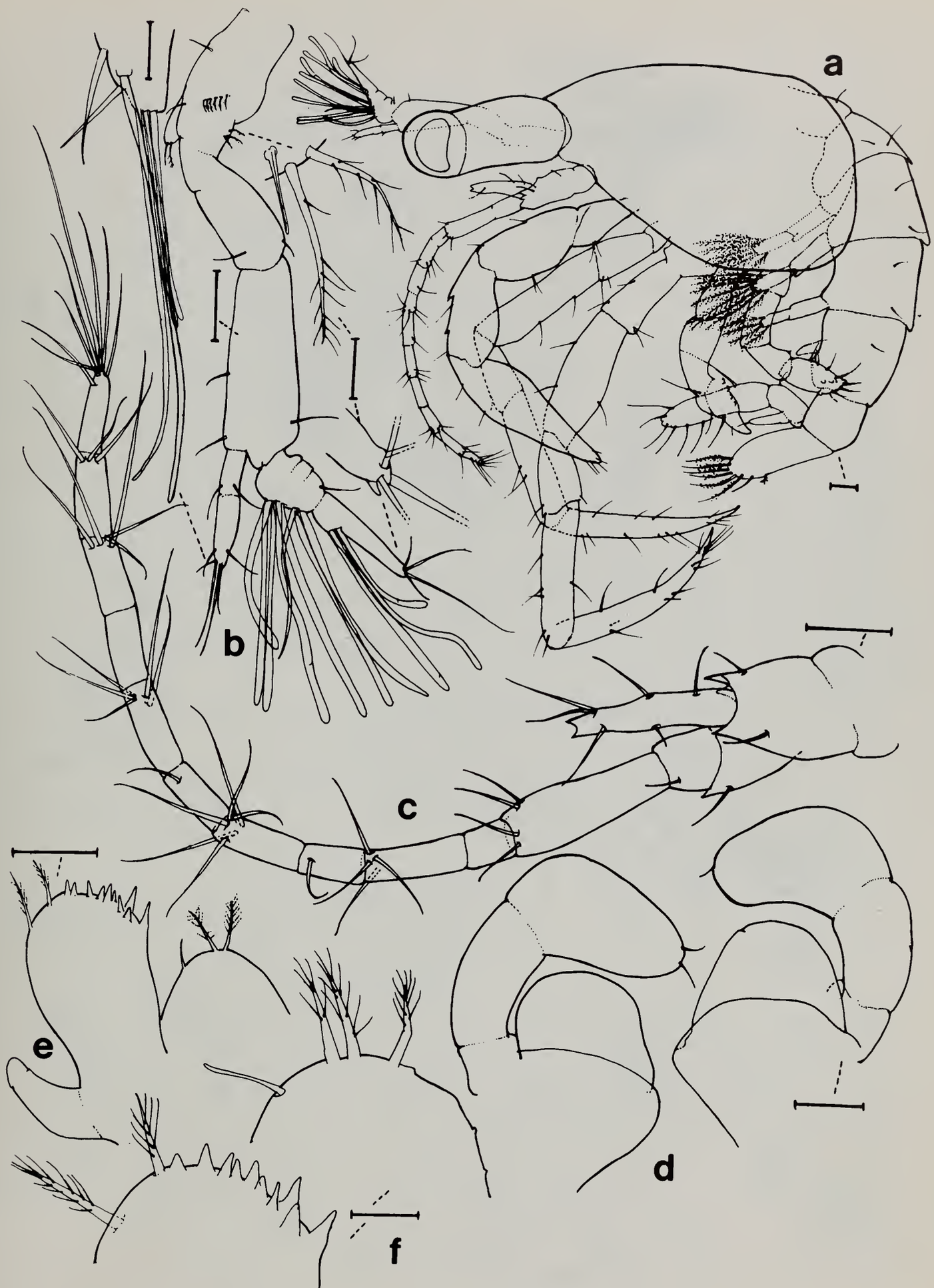

Fig. 9 *Anapagurus chiroacanthus* MEGALOPA: **a** whole larva from left lateral aspect; **b** left antennule; **c** left antenna; **d** mandibles from ventral aspect; **e** right maxillule; **f** basis & coxa of maxillule from another specimen. (Scales **a–c** = 100μm, **d, e** = 50μm, **f** & insets to **b** = 20μm).

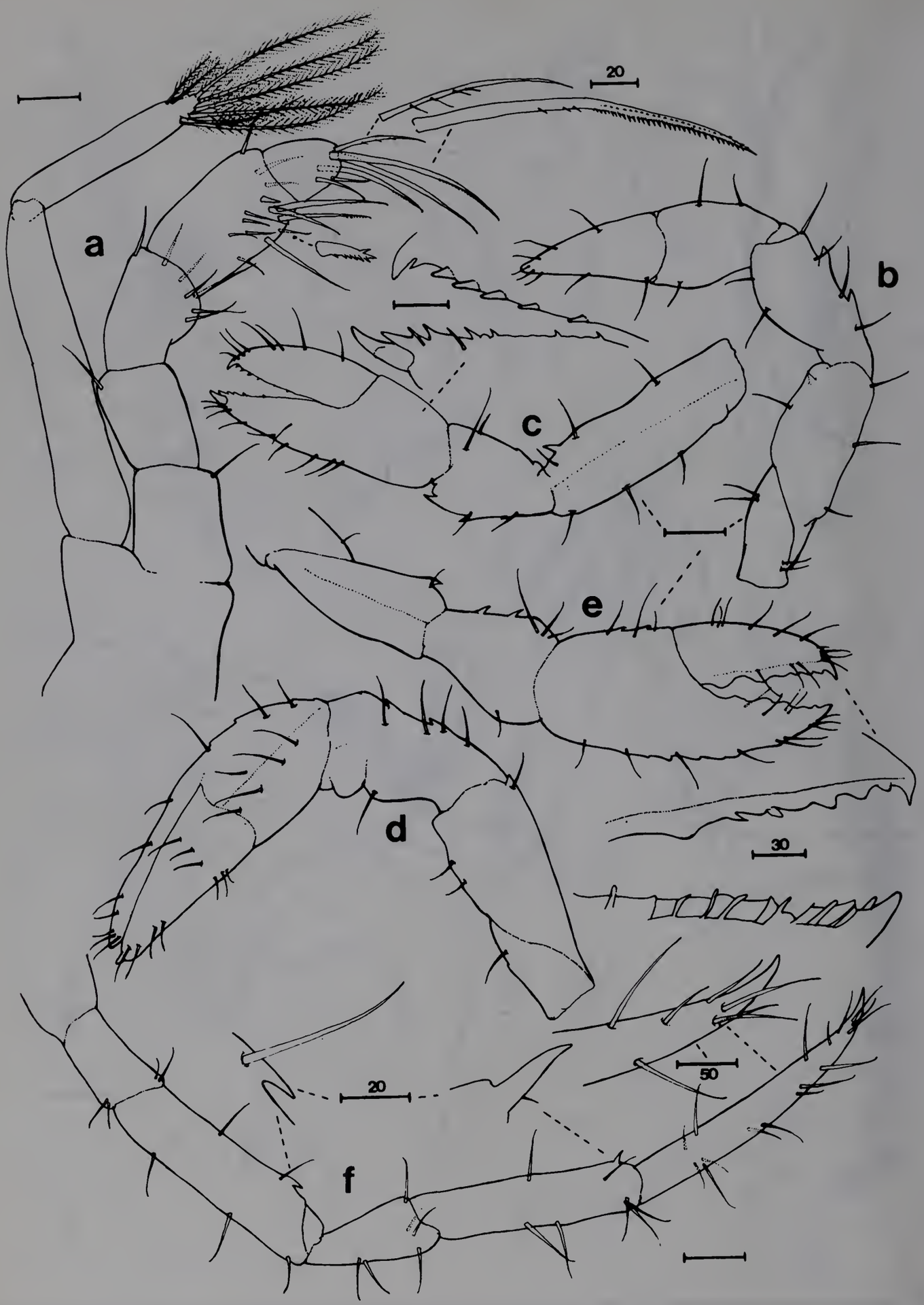

Fig. 10 *Anapagurus chiroacanthus* MEGALOPA: **a** right maxilliped 3; **b** left cheliped from dorsal and **c** outer aspect; **d** right cheliped from dorsal and **e** outer aspect; **f** left pereiopod 1. (Scales **a** = 50μm, **b–f** = 100μm, others as indicated).

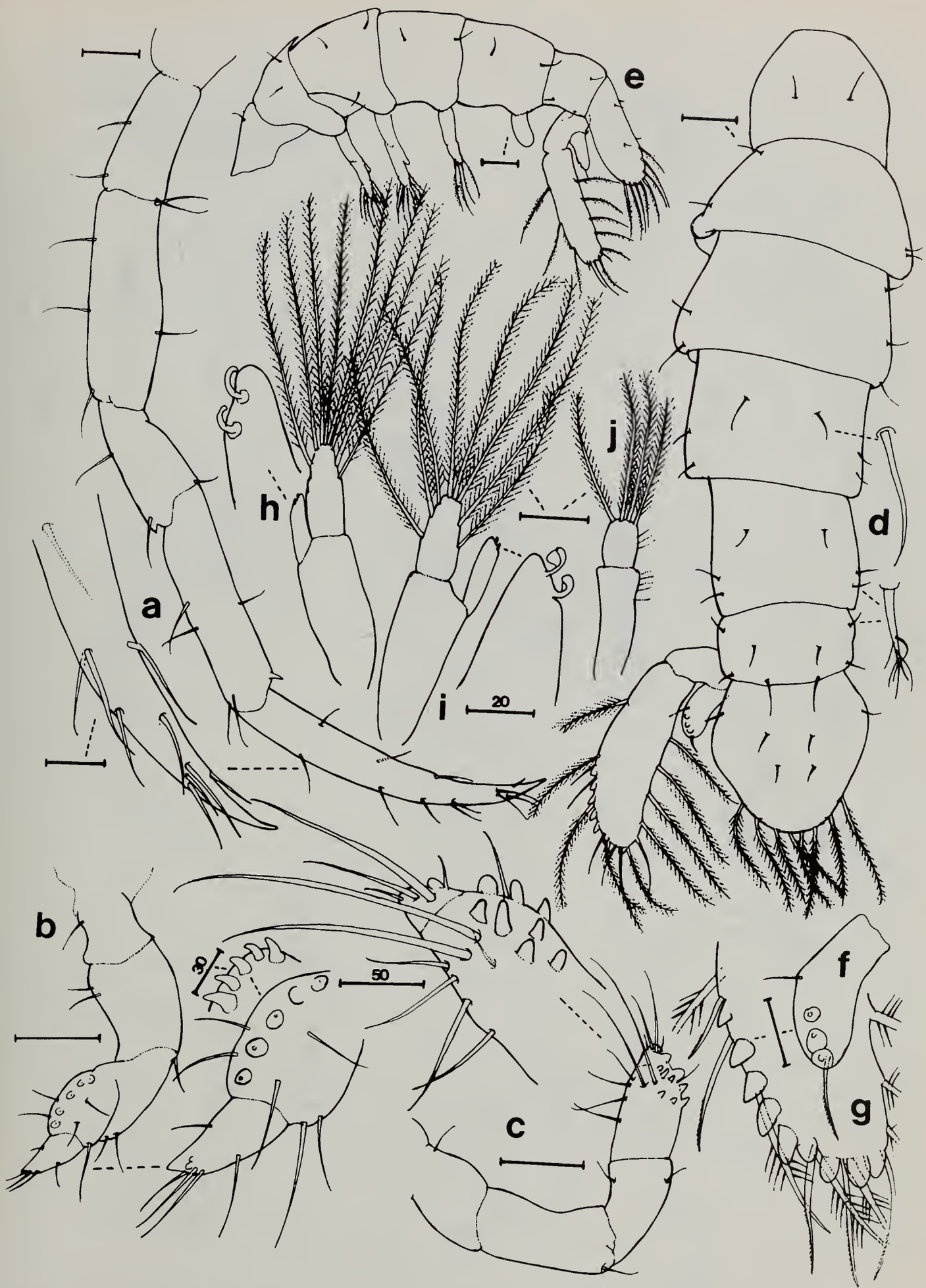

Fig. 11 *Anapagurus chiroacanthus* MEGALOPA: **a–c** left pereiopod 3–5; **d** abdomen telson & left uropod from dorsal and **e** from left lateral aspect; **f** endopod of left uropod and **g** distal part of exopod; *h–j* pleopods 1–3. (Scales **a, d, e, h–j** = 100μm, **b, c, f, g** = 50μm, others as indicated).

Fig. 12 *Anapagurus chiroacanthus* MEGALOPA: **a** gills, coxal segments of maxilliped 3 and pereiopods, CRAB 1: **b** anterior part of body; **c** right antennule; **d** antennular peduncle segment 1 from dorsal aspect; **e** right antennal peduncle from dorsal aspect and inset of acicle from ventral aspect; **f** mandibles from ventral aspect; **g** left maxillule. (Scales **a–c** = 100μm, **d–f** = 50μm, **g** = 30μm, others as indicated).

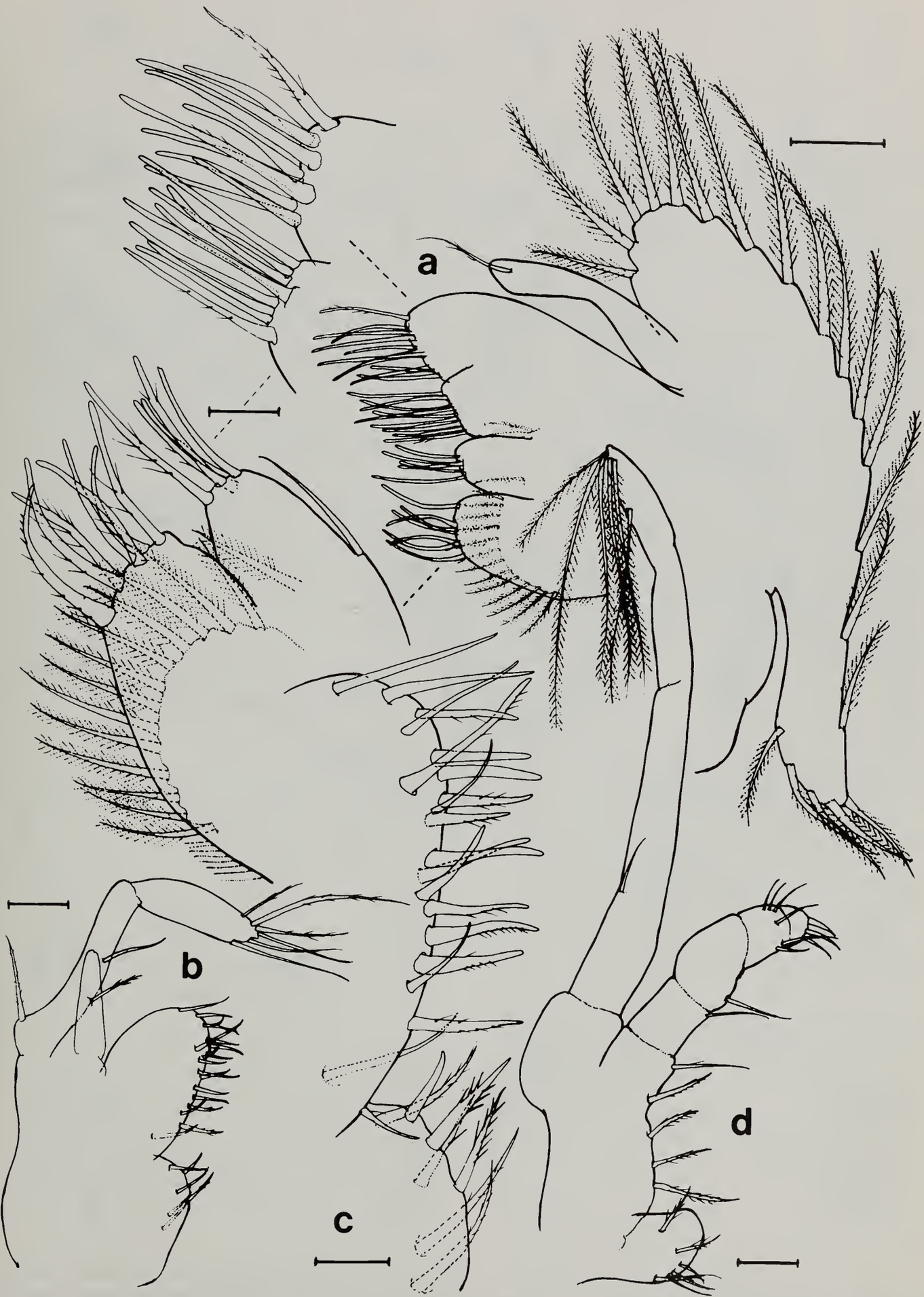

Fig. 13 *Anapagurus chiroacanthus* CRAB 1: **a** left maxilla; **b** right maxilliped 1; **c** basis & coxa of right maxilliped 1 from another specimen; **d** right maxilliped 2. (Scales **a, b, d** = 50μm, **c** & inset to **a** = 20μm).

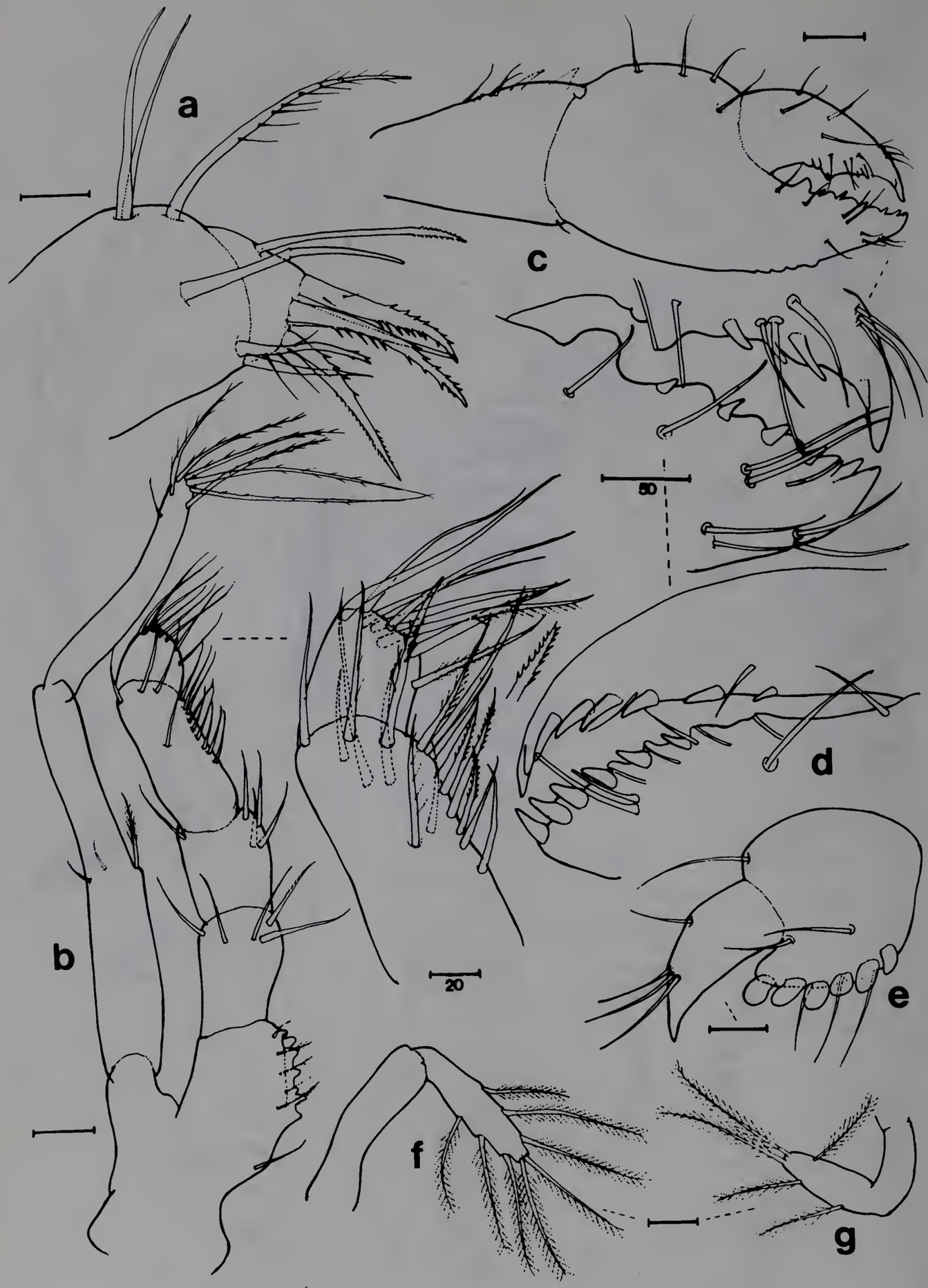

Fig. 14 *Anapagurus chiroacanthus* CRAB 1: **a** right maxilliped 2, dactyl & propodal endopod segments; **b** left maxilliped 3 (inset shows dactyl and propodus); **c** right pereiopod 1 (cheliped)-inset shows details of apposing dactyl and propodal distal margins; **d** distal apposing margins of left cheliped dactyl & propodus; **e** left pereiopod 4 dactyl and propodus; **f** left pleopod 1; **g** left pleopod 4. (Scales **a** = 30μm, **b, f, g** = 50μm, **c** = 100μm, **e** = 30μm, others as indicated).

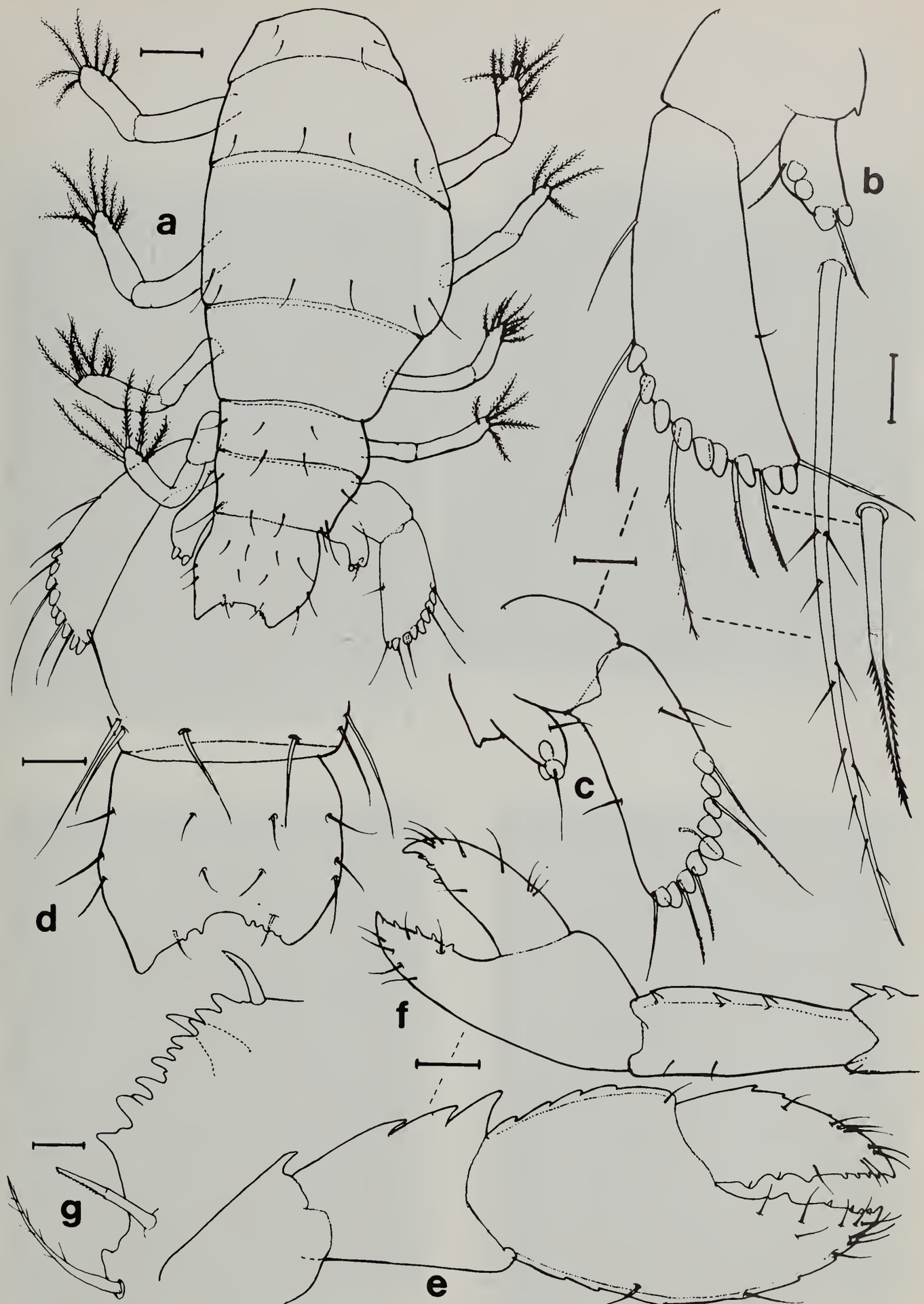

Fig. 15 *Anapagurus chiroacanthus* CRAB 1: **a** abdomen, telson and pleopods from dorsal aspect; **b** left uropod; **c** right uropod; **d** telson. CRAB 2: **e** right cheliped; **f** left cheliped; **g** ischium of maxilliped 3 from ventral aspect showing accessory tooth and *crista dentata*. (Scales, **a, e, f** = 100μm; **b–d** = 50μm, **g** & insets to **b** = 20μm).

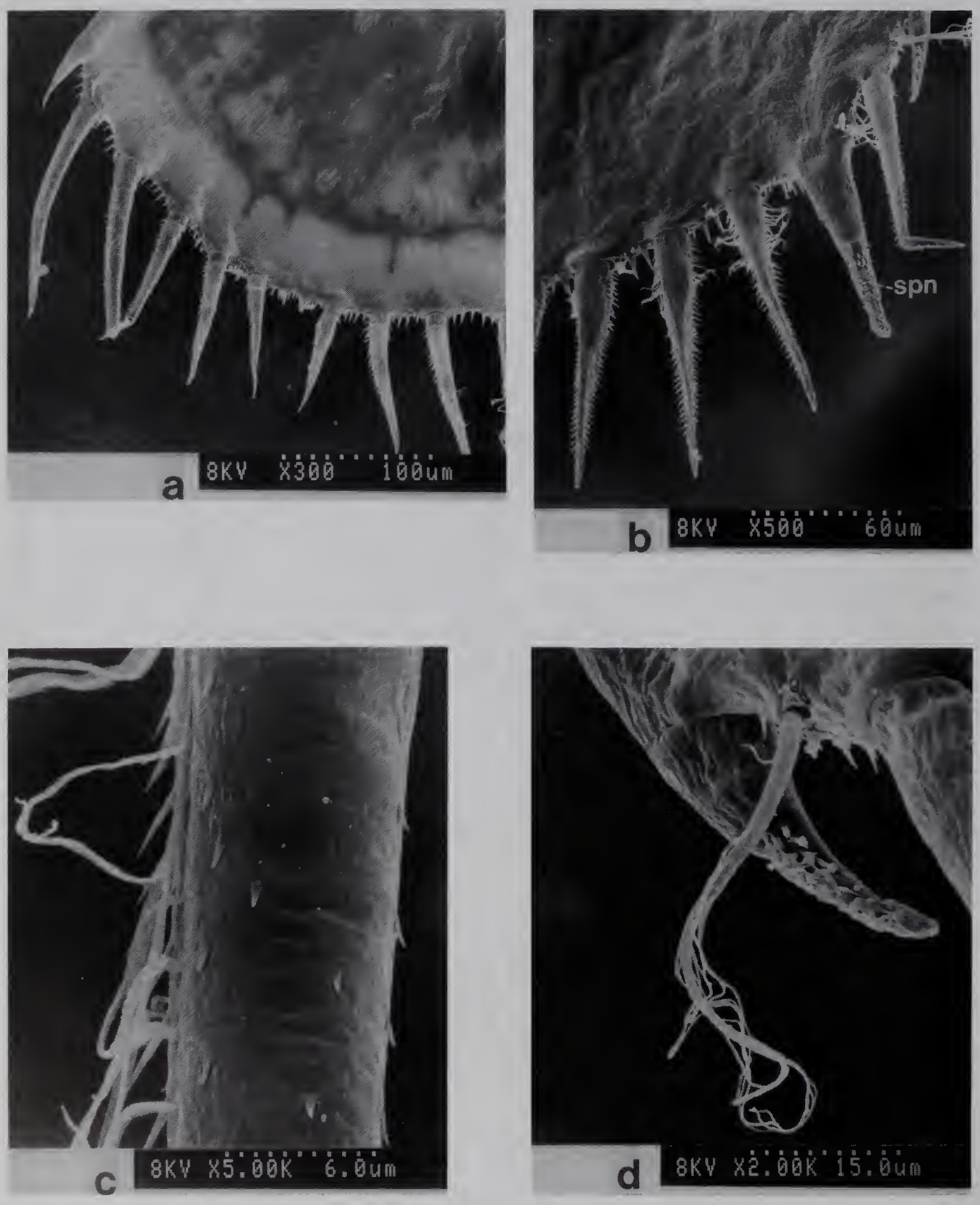

Fig. 16 *Anapagurus chiroacanthus* posterior margin of telson showing arrangement of setae in: **a** ZOEA I; **b** ZOEA III showing spine (*spn*) replacing 2nd plumodenticulate seta; **c** ZOEA I surface of one (5th) plumodenticulate seta; **d** details of pappose seta.

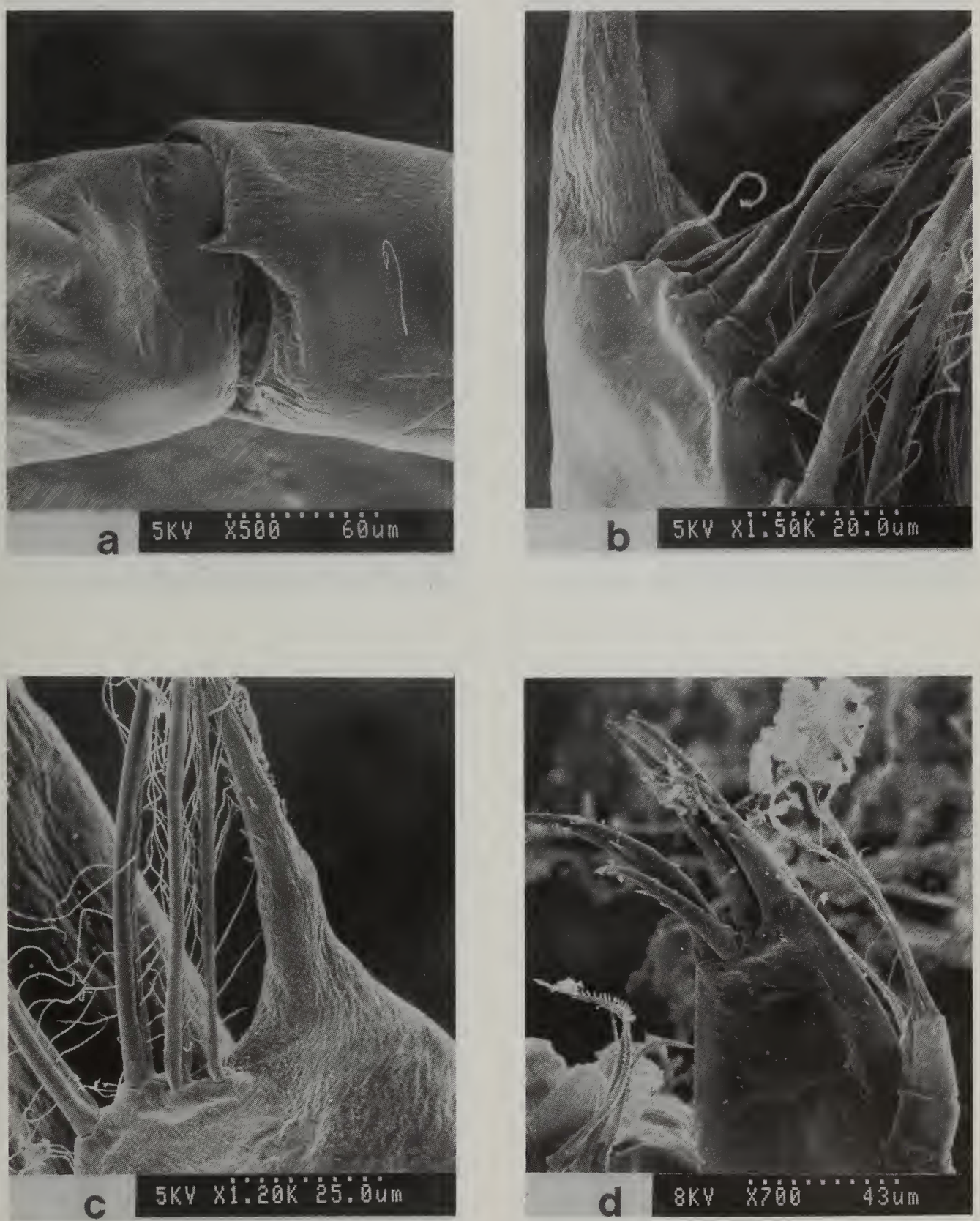

Fig. 17 *Anapagurus chiroacanthus* ZOEA I: **a** posterio-lateral spine on abdominal segment 5; **b** distal simple setae adjacent to antennal exopod spine; **c** same region of ZOEA II showing replacement of simple seta with plumose type; **d** ZOEA IV maxillule exopod and basis showing stout cuspidate setae.

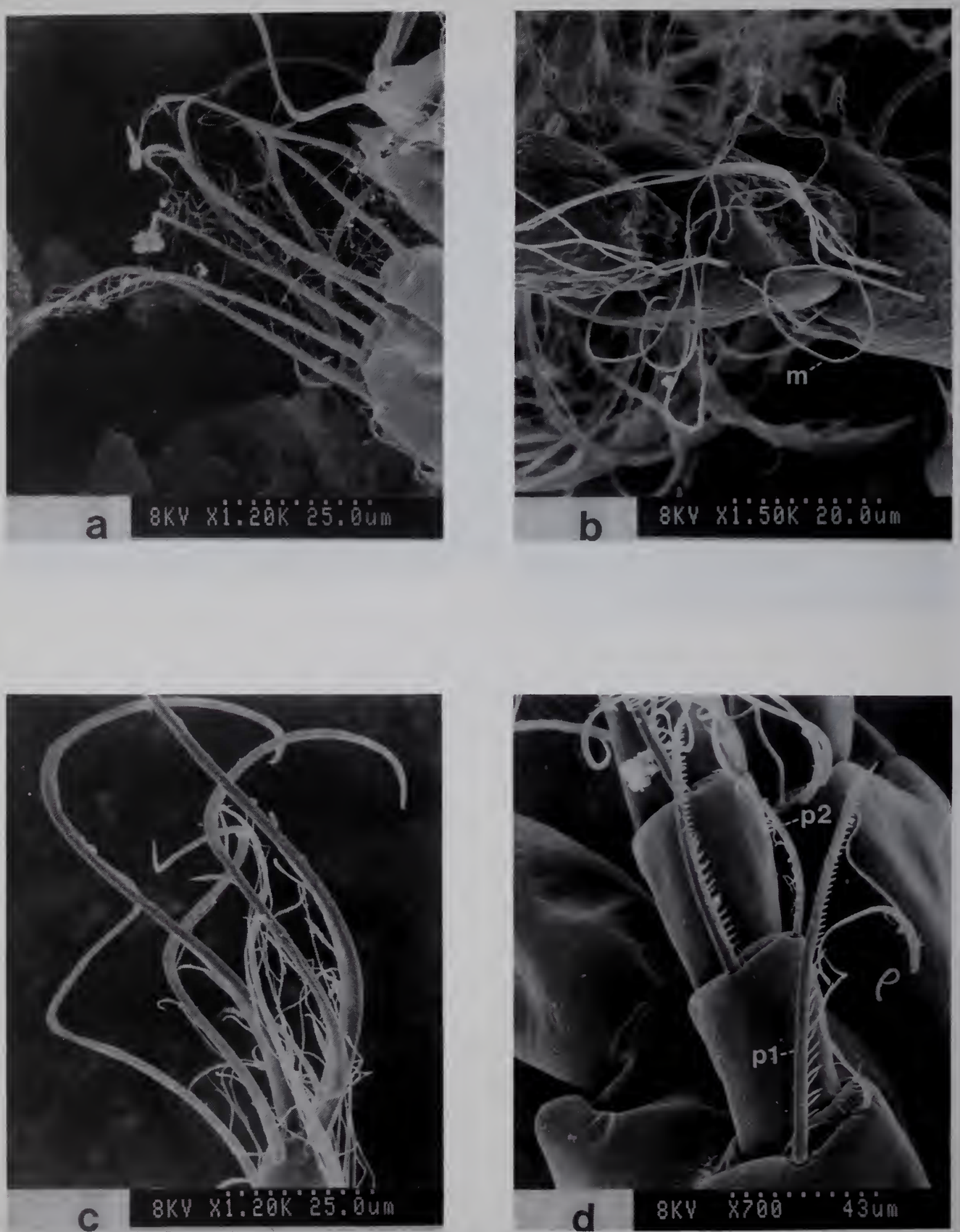

Fig. 18 *Anapagurus chiroacanthus* ZOEA I: **a** maxilla coxa showing plumodenticulate seta with long setules; **b** maxilliped endopod segments 2, 3 showing microtrichia (*m*) on outer surface. ZOEA IV **c** maxilliped 1 endopod segment 5 showing plumodenticulate setae variably invested with setules; **d** maxilliped 2, distal basis and endopod segments 1–3 showing two distinct types of plumodenticulate setae (p1, p2).

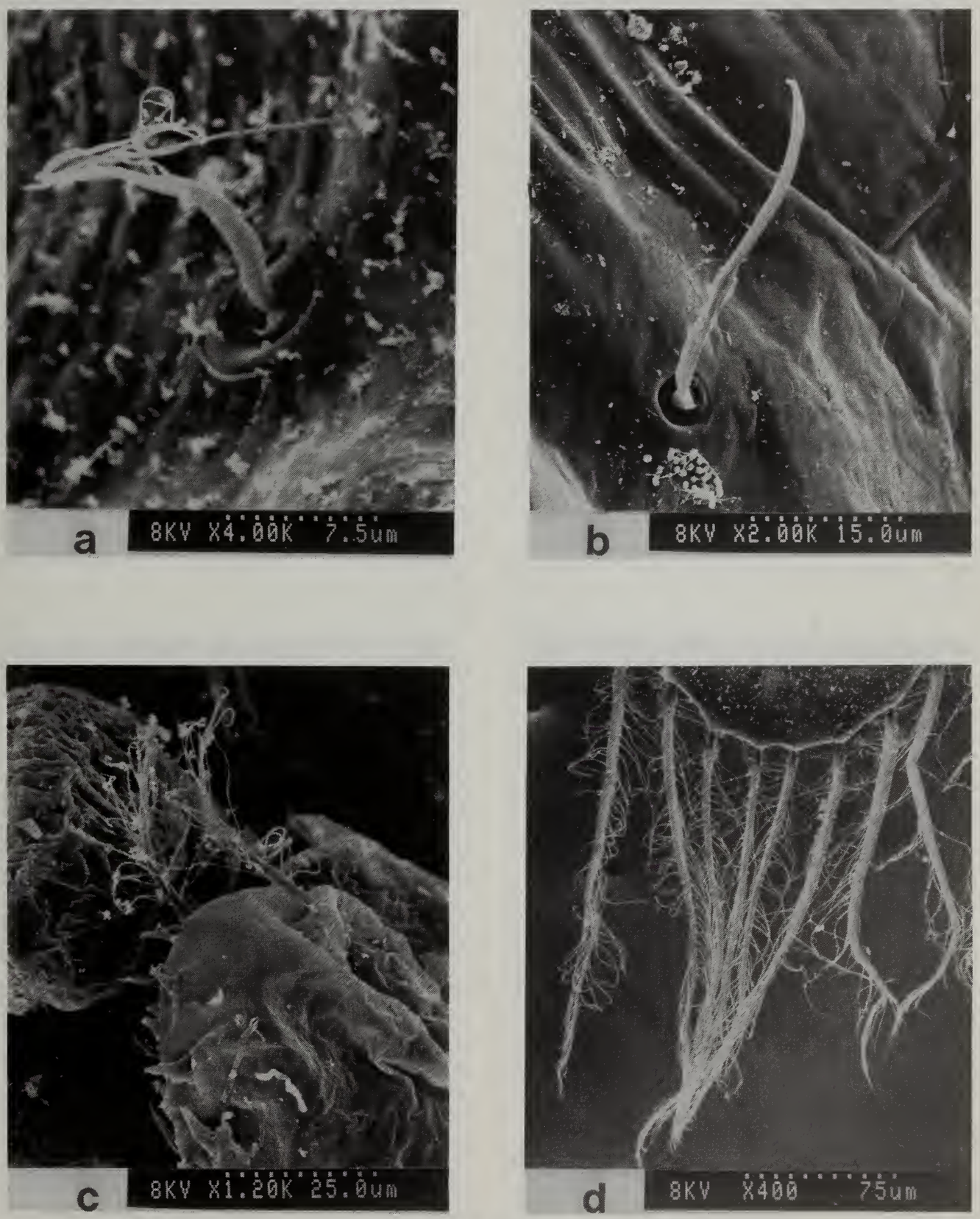

Fig. 19 *Anapagurus chiroacanthus* MEGALOPA: **a** abdominal segment 3 pappose seta; **b** abdominal segment 4 simple seta; **c** maxillule basis showing small spiniform setae; **d** plumose setae on telson posterior margin.

Fig. 20 *Anapagurus chiroacanthus* MEGALOPA: **a** maxilliped 3 distal inner propodus and dactyl showing two types of plumodenticulate setae (p1, p2); **b** pereiopod 2 proximal propodal dorsal surface showing simple (*s*) and pappose (*pa*) setae; **c** pereiopod 2 subdistal lower dactyl surface showing simple setae; **d** pereiopod 5 distal propodal surface and dactyl showing pseudochaetae (*pc*) and plumodenticulate (*p*) setae.

DISCUSSION

Ontogenetic variability of *A. chiroacanthus* larvae has not been studied previously and the apparent discrepancies between the account by Sars (1880) and the present material from Millport cannot be explained satisfactorily. Some of these differences may be due to omissions in drawing correct numbers of setae. The comparison suggests, however, that Sars' figures may represent more than two zoeal stages. For example, his figures of the first stage maxillipeds 1 and 2 show the endopod segments 1–4 each with a disto-external seta. In this stage of the present material only microtrichia are present on this region of some of these segments, but are replaced by setae at the second stage. He also shows the maxilla coxa with 3, 7 setae, a feature noted also for second stage specimens of the present material. Similarly, only 6 exopod setae are shown on the uropod exopod of his fourth stage; this is a feature of third stage zoeae of the present material, whereas 7 setae are present in all fourth stage specimens studied. The absence of setae on the maxilla scaphognathite posterior margin and the presence of 10 setae on the anterior part (compared with the 14 present in the fourth stage of the present material) suggests that Sars' figure of this appendage may represent a third stage zoea.

The slight differences noted between the present material and the brief descriptions of the larval stages of *A. chiroacanthus* by MacDonald *et al.* (1957) and Pike & Williamson (1959) perhaps reflect genotypic or phenotypic variability as their stages are undoubtedly correctly assigned and the average size at each stage of the present reared material from Millport agrees with the lower limit of the size ranges stated by these authors for the five larval stages. In their key to the identification of pagurid zoeae occurring in N.E. Atlantic waters, MacDonald *et al.* (1957) separate the zoeae of *Anapagurus* from those of other pagurids on the absence or the reduced posterio-lateral spine on abdominal segment 5 compared with the 'large lateral spines' on this segment in the other genera. In the reared material from Millport this posterio-lateral spine is well developed (see Fig. 17a) on segments 4 and 5 from the first to fourth zoeal stages. They were unable to find characters for separating the first zoeal stages of *A. chiroacanthus* from *A. hyndmanni* but used, as one of two features for distinguishing second stage zoeae of the species, the telson posterior margin 4th (ie 3rd plumodenticulate) seta which, in their material of *A. chiroacanthus,* was not longer than the 5th (ie 4th plumodenticulate) seta. However, second stage zoeae of the present material show some variability in this respect as some have this 3rd plumodenticulate seta noticeably longer than the 4th (see Fig. 3k) whereas in other specimens it ranges from being slightly shorter to subequal to the 4th on one half of the telson to slightly longer than the 4th on the opposite side. As mentioned previously, the fourth stage of the present material is without a pleopod bud on segment 4. The bud was present in this stage of *A. chiroacanthus* material studied by MacDonald *et al.* (1957) and was used, with other characters, for separating the fourth stage of this species from *A. hyndmanni.* The reduced or absent posterio-lateral spines on the fifth abdominal segment and the presence of an incipient pleopod 3 on segment 4 were also used in later revised keys by Pike & Williamson (1959: 1960) to separate zoeae of N.E. Atlantic/ Mediterranean *Anapagurus* species from those of other pagurids. In these keys *A. chiroacanthus* is distinguished by having the rostrum projecting beyond the spine of the antennal exopod (scaphocerite) by about the length of the spine in the first and second stages and in having the innermost telson spine* shorter than either the 1st or 3rd plumodenticulate seta in the third and fourth stages. These are also features of the reared material from Millport. The partial regression of the first pair of pleopods noted in the two specimens studied of the second stage crab suggests that these may be males, although there is no evidence of gonopores or development of a coxal tube on the left pereiopod 5 characteristic of male *Anapagurus.* This assumption is based on the known state of pleopod development of later stage juveniles and also adults in which males have only uniramous second to fourth pleopods present on the left side of the abdomen; in females the first to fourth pleopods on the left side are biramous, although a uniramous pleopod 4 is occasionally present on the right side. Post-larval pleopod development has been studied in only a few pagurids. The first crab stage of *Clibanarius sclopetarius* Herbst and *C. vittatus* (Bosc), for example, has the left and right of the four paired pleopods equal in size (see Brossi-Garcia 1987*a*; 1988) whereas in *Dardanus pectinatus* (Ortmann) those on the right are smaller than those on the left (Forest 1954); a similar situation is just discernible in *Anapagurus chiroacanthus* (see Fig. 15a). In *Clibanarius,* sexual differentiation appears to occur only after the fifth stage crab. The pleopods are biramous and in the male the endopod remains small, but in females grows to equal the exopod length. Also, in the two species of *Clibanarius* mentioned the loss of pleopods from the right side of abdomen occurs through the second to fourth stages (Brossi-Garcia 1987*a*: 1988) whereas in *Clibanarius erythropus* (Latreille) they have disappeared by the second stage (Dechancé & Forest, 1958), a situation also apparent in *A. chiroacanthus.* By comparison, three pairs of symmetrical pleopods were reported as still present in a second stage crab designated *Anapagurus* species N.1 by Pike & Williamson (1960) and later assigned to *A. petiti* by Dechancé & Forest (1962). The occasional pairing of the fourth pleopods in adult females of *A. chiroacanthus* requires further study as it is not known whether the fourth pleopod on the right side is retained throughout post-larval development of this sex or is secondarily acquired at some later stage. Re-acquisition of pleopods (in this case the second pair) is known to occur in males of *Paguristes sericeus* A. Milne Edwards following their loss in the early juvenile stages (see Provenzano & Rice, 1964).

Provenzano (1971: 249) suggested there is '... great similarity between the described larvae of *Anapagurus, Catapaguroides, Orthopagurus* and the relatively large number of larvae of *Pagurus* so far described, although within the last genus, there is a diversity of forms ...' The larval development of *Orthopagurus* is known only from the brief account by Hart, (1937) of the terminal zoeal and megalopal stage of *Orthopagurus schmitti* (Stevens), whereas the complete larval development of *Cestopagurus* (previously *Catapaguroides*)

* This process is termed '3rd telson spine' by Pike & Williamson (1959: 7). In this present study the processes on each half of the telson posterior margin are considered to be composed of: (i) an outermost furca, developed as a spiniform or cuspidate seta in *Anapagurus* but present as fixed spines in other pagurids; (ii) an adjacent pappose type seta; (iii) a number of plumodenticulate type setae. From the third stage the 2nd innermost plumodenticulate seta is replaced by a spine in many pagurids and is here designated as the 'innermost telson spine'.

timidus (Roux) was well described by Dechancé (1961). It appears possible to distinguish the terminal zoeal stage of *O. schmitti, C. timidus* and *A. chiroacanthus* using the following limited combined features:

Orthopagurus schmitti: (i) *carapace* posterio-lateral spine not produced but broadly angular; (ii) *telson* length about ×2 width, 2nd ?plumodenticulate seta on posterior margin longest and not developed as spine; (iii) *uropod* endopod without setae and exopod with several inner distal spines.

Cestopagurus timidus: (i) *carapace* posterior-lateral spine not produced, broadly angular; (ii) *telson* length about 1½× width and with 2nd plumodenticulate seta on posterior margin developed as spine and longest; (iii) *uropod* endopod with 1–2 setae and exopod without inner distal spines.

Anapagurus chiroacanthus: (i) *carapace* posterio-lateral spine small but produced, not broadly angular; (ii) *telson* length about 1½× width and with 2nd plumodenticulate seta on posterior margin developed as spine but not longest; (iii) *uropod* endopod with 1 seta and exopod without inner distal spines.

The detailed account by Dechancé (1961) of *Cestopagurus timidus* larval development enables satisfactory comparisons to be made with corresponding stages of *Anapagurus chiroacanthus* to which genus it may be phylogenetically closest. The zoeal stages of this species differ from those of *C. timidus* as follows: *Zoea I* (i) *antennule*: only 1 plumose seta present in *A. chiroacanthus* in addition to aesthetascs (*cf. 3* plumose setae in *C. timidus*); (ii) *maxillule*: endopod segment 3 with only 2 setae (*cf.* 3 setae), basis without plumodenticulate setae (*cf.* with setae); (iii) *maxilla*: basis with 4,4 (*cf.* 4,5); (iv) *maxilliped 1*: basis with a total of 8 setae on inner margin (distributed differently from those on this margin of *C. timidus* which has 10 setae), microtrichia present on outer margins of endopod segments 2–4 (not reported for *C. timidus*); (v) *maxilliped 2*: without mid-point seta on inner margin of basis (present in *C. timidus*), microtrichia present on outer margin of endopod segment 3 (not reported for *C. timidus*); (vi) *telson*: posterior margin without median notch (*cf.* with notch). *Zoea II* (i) *antennule*: only one plumose seta present (*cf.* 2); (ii) *Maxillule*: basis with only one small simple seta (*cf.* 2 setae); (iii) *maxilla*: scaphognathite with 7 (*cf.* 8 setae) and coxa with 3,7 setae (*cf.* 4,7); (iv) *maxilliped*: 1 endopod inner margin segment 1 with 3 setae (*cf.* 2 setae); (v) *maxilliped* 3: endopod undeveloped (*cf.* developed and with 2 setae); (vi) *pleopod*-uropod: buds incipient (*cf.* not visible). *Zoea III* (i) *antennule*: only 3 plumose seta (*cf.* 6); (ii) *maxilla*: scaphognathite with 9 setae (*cf.* 8), basis with 4,5 setae (*cf.* 5,5); (iii) *maxilliped* 1: endopod inner margin of segment 1 with 3 setae (*cf.* 2); (iv) *maxilliped* 3: endopod bud without setae (*cf.* 2 setae); (v) *abdomen*: segment 5 posterio-lateral spines small (*cf.* larger); (vi) *pleopods*: endopods of uropods barely perceptible (*cf.* conspicuous buds); (vii) *telson*: with a pair of dorsal setae (*cf.* without dorsal setae), innermost telson spine about one fifth telson length (*cf.* one third) and anal spine absent (*cf.* present). *Zoea IV* (i) *maxillule*: coxa with 9 setae (*cf.* 8); (ii) *maxilla*: scaphognathite with 16 marginal setae, 4 on distal lobe (*cf.* 11 setae, none on distal lobe); (iii) *telson*: with 2 pairs of dorsal setae (*cf.* without setae), innermost telson spine about one ninth telson length (*cf.* one fifth telson length), anal spine absent (*cf.* present); (iv) *pleopod*: endopod of uropod with 1 seta (*cf.* 2 setae).

The megalopal stage of *Anapagurus chiroacanthus* can be distinguished from that of *C. timidus* (see Dechancé & Forest, 1958) in having: (i) *carapace*: of *A. chiroacanthus* with more acute rostral and subacute lateral projections; (ii) *eyes*: with proportionally longer eyestalks; (iii) *antenna*: with 10-segmented flagellum (*cf.* 7); (iv) *maxilla*: scaphognathite and basial endites with greater numbers of setae (25 marginal setae on scaphognathite and 8,7 on basis *cf.* 22 and 3,5); (v) *maxilliped* 2: exopod segment 2 with 6 setae (*cf.* 4) and endopod less developed i.e. (2-segmented *cf.* 5 segmented); (vi) *maxilliped* 3: exopod segment 2 with 8 setae (*cf.* 4); (vii) *pereiopod* 3: dactyl inner margin without spiniform setae (*cf.* 3); (viii) *pereiopod* 5; fewer pseudochaetal type setae on propodus; (ix) *pleopod* 4: only incipient (*cf.* well developed and with exopodal setae); (x) *pleopods*: endopod of uropod with one distal seta (*cf.* 3); (xi) *telson*: dorsal surface with 2 pairs of setae (*cf.* 3).

Of the numerous combined larval characters suggested by MacDonald *et al.* 1957 for distinguishing *Anapagurus* from those of *Pagurus*, only one, *viz.* less than 4 pairs of fully developed pleopods in the terminal zoeal stage and megalopa, can be considered exclusive for separating these two genera now that the larval morphology is known for a number of additional species of *Pagurus* (see Nyblade & McLaughlin, 1975 for references and also Tirmizi & Siddiqui, 1980; Hebling & Brossi-Garcia, 1981; Hong, 1981; Negreiros-Fransozo, 1984; Konishi & Quintana, 1987; McLaughlin & Gore 1988; McLaughlin *et al.* 1988). Features for separating the four groups of *Pagurus* larvae were reviewed by McLaughlin & Gore (1988: table I). Applying these to *Anapagurus* may allow the larvae of this genus to be distinguished from those of *Pagurus* on the following combined features. *Zoea*: (i) *carapace* of *Anapagurus* not elongated; (ii) *abdominal* segment 5 with short posterio-lateral spine, dorso-median spine on segment 6 absent; (iii) *telson* broad, '4th' (ie. 2nd plumodenticulate) seta developed as a spine from third zoeal stage and less than one half telson width; (iv) *Antenna*-endopod with 2 setae in ZI & II, exopod with curved outer margin, length less than ×3 width and with 9–10 setae; (v) *mandible*-palp absent; (vi) *pleopods* developed as buds only on segments 2 & 3 in stage IV zoea, uropod endopod with 1 seta. *Megalopa*: (i) *antenna*-flagellum reaching to or just beyond extremities of chelipeds; (ii) pleopods fully developed only on segments 2–4; (iii) *colour*-yellow chromatophore over stomach present.

It is not easy to distinguish plesiomorphic from apomorphic characters of pagurid larvae. Meristic studies of *A. chiroacanthus* suggest that the zoeae of this species are less plesiomorphic than *C. timidus* if reduction of setal numbers and their types on limb endites implies a more derived state. Whereas features such as the presence of telson dorsal setae, the retention of furcal spiniform/cuspidate setae (see below), the developed setae on the scaphognathite posterior margin and the relatively shorter innermost telson spines may be apomorphic characters of *A. chiroacanthus* zoeae. However, the megalopa of *A. chiroacanthus* has slightly greater numbers of setae and the antennal flagellum has more segments when compared with *C. timidus* but this condition may reflect the slightly larger overall size of *A. chiroacanthus* megalopa. Many other features of *A. chiroacanthus* megalopal stage (i.e. absence of spiniform setae on inner margins of dactyls of second and third pereiopod; fewer pseudochaetal type setae on propodal surface of the fifth pereiopod; fourth pleopod only incipiently developed and uropod

endopod with only one seta; dorsal surface of telson with two pairs of setae) perhaps suggests a more derived condition that obtains for the related *C. timidus*, but it is debatable if all these features are truly apomorphic.

The types of setae on the body and limb endites of larval pagurids has received scant attention. The terminology used in this study to classify setae on *A. chiroacanthus* follows the schemes proposed by Drach & Jacques (1977) and Pohle & Telford (1981) with the exception of subdivisions of the plumodenticulate categories proposed by the latter. The types of setae noted on body surfaces and appendages are mentioned in the descriptive account (p. 00) and aspects related to ontogeny are noted here. The transformation of one type of seta into another or the replacement of one type by another is particularly evident at the moult from terminal zoeal stage to megalopa. For example, this change is obvious when setae on the telson posterior margin of the last zoeal stage and megalopa are compared. These change from a stout zoeal plumodenticulate type into a thin megalopal plumose type, accompanied by the total disappearance of the telson spiniform/cuspidate furcal setae and the adjacent (pappose) seta. The telson furcae are developed as spiniform/cuspidate setae in all zoeal stages of *A. chiroacanthus* as correctly shown by Sars (1890), but not by MacDonald *et al.* (1957) who illustrate these processes as fixed spines. However, fixed furcal spines are recorded as present throughout the zoeal development of a number of pagurids e.g. *Paguristes, Petrochirus, Diogenes, Cestopagurus* and some *Pagurus* species (see Rice & Provenzano, 1965; Provenzano, 1968; Baba & Fukuda, 1985; Dechancé, 1961; Nyblade & McLaughlin, 1975: 286; Hong, 1981; MacLaughlin *et al.* 1988 & MacLaughlin & Gore, 1988). By comparison, these furcal processes of other pagurids appear to be developed as spiniform setae in all stages e.g. *Clibanarius, Labidochirus, Calcinus, Pylopaguropsis, Phimochirus* and some *Pagurus* species (see Lang & Young, 1977; Nyblade & McLaughlin, 1975; Provenzano, 1962; Provenzano, 1971; Gore & Scotto, 1983). But for one species, *Lithopagurus yucatanicus,* there is a suggestion that the furcal spines become transformed into setae in later stages (see Provenzano, 1968*a*, Fig. 7). The transition of the '3rd' (i.e. 2nd plumodenticulate) telson seta into a spine occurs in the late zoeal stages of many pagurid species having either furcal spiniform setae or furcal spines, whereas in a more limited number the '3rd' telson seta is never replaced by a spine and this feature may be indicative of an apomorphic condition, as suggested by Gore & Scotto (1983).

The transformation of the maxillule basis from a narrowed endite bearing stout cuspidate setae in the zoea, to a broad endite armed with small spiniform setae in the megalopa, and the total disappearance of the stout plumose setae and their replacement by simple setae on the antennal exopod during the moult from terminal zoeal stage to megalopa, are also examples of setal transformations. Less obvious, perhaps, is the replacement of the simple seta adjacent to the antennal exopod disto-external spine, with a plumose type during the moult from first to second stage zoea. This type of change occurs also in the development from first to second stage of other pagurids e.g. *Cestopagurus timidus* (Dechancé, 1961), *Calcinus tibicens* (Provenzano, 1962), *Pagurus alatus* (Bookhout, 1972), and *P. dubius* (Hong, 1981) but is clearly not the case for others. Finally, a feature worth noting is the maximum number of sub-distal setae acquired on the ventral surface of the zoeal maxillule basis. These are absent in all stages of the Millport reared material of *A. chiroacanthus* and may be absent also in some species of *Pagurus* (e.g. they are not shown in figures of the maxillule of *Pagurus maclaughlinae* by MacLaughlin & Gore 1988). Only one seta occurs in *Diogenes nitidimanus* (Baba & Fukuda, 1985), *Pagurus prideaux, P. alatus* and *P. variabilis* (Goldstein & Bookhout, 1972; Bookhout, 1972; Samuelsen, 1972) whereas two are present in many other pagurids.

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REFERENCES

Baba, K. & Fukuda, Y. 1985. Larval development of the Hermit Crab *Diogenes nitidimanus* Terao, 1913 (Crustacea: Anomura: Diogenidae) reared in the laboratory. *Memoirs of the Faculty of Education, Kumamoto University, Natural Sciences, Kumamoto* **34**: 5–17.

Bookhout, C. G. 1972. Larval development of the Hermit Crab, *Pagurus alatus* Fabricius, reared in the laboratory (Decapoda, Paguridae). *Crustaceana, International Journal of Crustacean Research, Leiden* **22** (3): 215–238.

Brossi-Garcia, A.L. 1987. Morphology of the larval stages of *Clibanarius sclopetarius* (Herbst, 1796) (Decapoda, Diogenidae) reared in the laboratory. *Crustaceana, International Journal of Crustacean Research, Leiden* **52** (3): 251–275.

—— 1987*a*. Juvenile development of *Clibanarius sclopetarius* (Herbst, 1796) (Crustacea: Paguridea: Diogenidae) in the laboratory. *Journal of Crustacean Biology, Washington, D.C.* **7** (2): 338–357.

—— 1988. Juvenile development of *Clibanarius vittatus* (Bosc, 1802) (Decapoda, Anomura), in the laboratory, *Crustaceana, International Journal of Crustacean Research, Leiden* **54** (3): 294–313.

Dechancé, M. 1961. Sur la morphologie external des larves de Pagurides, I. *Catapaguroides timidus* (Roux). *Crustaceana, International Journal of Crustacean Research, Leiden* **2** (1): 53–67.

—— **& Forest, J.** 1958. Les glaucothoés de *Catapaguroides timidus* (Roux) et de *Clibanarius erythropus* (Latreille), remarques sur le stade post-larvaire des Pagurides. *Bulletin de la Société Zoologique de France, Paris* **83** 2–3: 274–293.

—— & —— 1962. Sur *Anapagurus bicorniger* A. Milne Edwards et E. L. Bouvier et *A. petiti* sp. nov. *Bulletin du Museum National d'Histoire Naturelle, Paris* (2) **34** 4: 293–307.

Drach, P. & Jacques, F. 1977. Système sétifère des Crustacés Décapodes. Principes d'une classification générale. *Compte Rendu hebdomadaire des Séances de l'Academie des Sciences, Paris* (D) **284**: 1995–1998.

Forest, J. 1954. Morphogenèse—Sur les premiers stades post-larvaires du Pagure *Dardanus pectinatus* (Ortmann). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences,* Paris **239**: 1697–1699.

Goldstein, B. & Bookhout, C. G. 1972. The larval development of *Pagurus prideauxi* Leach, 1814, under laboratory conditions (Decapoda, Paguridea). *Crustaceana, International Journal of Crustacean Research, Leiden* **23** (3): 263–281.

Gordan, J. 1956. A Bibliography of Pagurid Crabs, exclusive of Alcock, 1905. *Bulletin of the American Museum of Natural History, New York* **108** 3: 257–352.

Gore, R. H. & Scotto, L. E. 1983. Studies on Decapod Crustacea from the Indian River region of Florida XXVII. *Phimochirus holthuisi* (Provenzano, 1961) (Anomura: Paguridae): The complete larval development under laboratory conditions, and the systematic relationships of its larvae. *Journal of Crustacea Biology, Washington, D.C.* **3** (1): 93–116.

Gurney, R. 1942. *Larvae of Decapod Crustacea.* Ray Society, London i–vi + 306pp.

Hart, J. F. L. 1937. Larval and adult stages of British Columbia Anomura. *Canadian Journal of Research, Ottawa* D **15**: 179–220.

Hebling, N. J. & Brossi-Garcia, A. L. 1981. Desenvolvimento pósembrionário de Pagurus criniticornis (Dana, 1852) (Crustacea, Paguridae), em laboratório. *Revista Brasileira de Biologia, Rio de Janeiro* **41**: 765–779.

Hong, Sung Yun. 1981. The larvae of *Pagurus dubius* (Ortman) (Decapoda, Paguridae) reared in the laboratory, *Bulletin of National Fisheries of Busan, Busan, Korea* **21** 2: 1–11.

Konishi, K. & Quintana, R. 1987. The larval stages of *Pagurus brachiomastus* (Thallwitz, 1892) (Crustacea: Anomura) reared in the laboratory, *Zoological Science, Zoological Society of Japan,* Tokyo **4**: 349–365.

Lang, W. H. & Young, A. M. 1977. The larval development of *Clibanarius vittatus* (Bosc) (Crustacea: Decapod: Diogenidae) reared in the laboratory. *Biological Bulletin, Marine Biological Laboratory Woods Hole, Mass* **52** 84–104.

Lilljeborg, W. 1855. Om Hafs-Crustaceer vid Kullaberg i Skane, öfversigt af Kongl. *Vetenskaps-Akademiens Förhandlingar, Stockholm* **12**: 117–138.

MacDonald, J. D., Pike, R. B. & Williamson, D. I. 1957. Larvae of the British species of *Diogenes, Anapagurus* and *Lithodes* (Crustacea Decapoda). *Proceedings of the Zoological Society of London* **128** 2: 209–257.

Martin, J. W. 1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeae of the western Atlantic and Gulf of Mexico. *Bulletin of Marine Science and Caribbean, Coral Gables* **24** (2): 220–239.

McLaughlin, P. A. & Gore, R. H. 1988. Studies on the *provenzanoi* and other pagurid groups: I. The larval stages of *Pagurus maclaughlinae* Garcia-Gomez, 1982 (Decapoda: Anomura; Paguridae), reared under laboratory conditions, *Journal of Crustacean Biology, Washington, D.C.* **8** (2): 262–282.

——, —— **& Crain, J. A.** 1988. Studies on the *provenzanoi* and other pagurid groups: II. A re-examination of the larval stages of *Pagurus hisutiusculus hirsutiusculus* (Dana) (Decapoda: Anomura: Paguridae) reared in the laboratory, *Journal of Crustacean Biology, Washington D.C.* **8** (3): 430–450.

Negreiros-Fransozo, M. L. 1984. Desenvolvimento pós-embrionario de *Pagurus brevidactylus* [Stimpson, 1858], *Panopeus americanus* Saussure, 1857 e *Euryanpanopeus abbreviatus* [Stimpson, 1860] [Crustacea, Decapoda], em laboratório. Unpublished thesis, Universidade Estadual Paulista 'Julio de Mesquita Filho', São Paulo, Brazil, pp. 1–121 (not seen).

Nyblade, C. F. & McLaughlin, P. A. 1975. The larval development of *Labidochirus splendescens* (Owen, 1893) (Decapoda, Paguridae). *Crustaceana, International Journal of Crustacean Research, Leiden* **29** (3): 271–289.

Pike, R. B. & Williamson, D. I. 1959. Zooplankton Sheet 81, Crustacea Decapoda: Larvae XI Paguridea, Coenobitidea, Dromiidea, and Homolidea, 1958 (revised 1959). *Fiches d'Identification du Zooplancton, Conseil Permanent International pour l'Exloration de la Mer,* Copenhagen: 9 pp.

—— **&** —— 1960. Larvae of Decapod Crustacea of the families Diogenidae and Paguridae from the Bay of Naples. *Pubblicazioni della Stazione Zoologica di Napoli, Milano & Napoli* **31** 3: 493–552.

Pohle, G. & Telford, M. 1981. Morphology and classification of crustacean larval setae: a scanning electron microscope study of *Dissodactylus crinitichelis* Moriera, 1901 (Brachyura: Pinnotheridae). *Bulletin of Marine Science, Coral Gables* **31** (3): 736–752.

Provenzano, A. J. 1962. The larval development of *Calcinus tibicen* (Herbst) (Crustacea, Anomura) in the laboratory. *Biological Bulletin, Marine Biological Laboratory Woods Hole, Mass.* **123** 1: 179–202.

—— 1968. The complete larval development of the West Indian hermit crab *Petrochirus diogenes* (L.) (Decapoda, Diogenidae) reared in the laboratory. *Bulletin of Marine Science, Coral Gables* **18** 1: 143–181.

—— 1968*a*. *Lithopagurus yucatanicus,* a new genus and species of Hermit Crab with a distinct larva. *Bulletin of Marine Science, Coral Gables* **18** 3: 627–644.

—— 1971. Zoeal development of *Pylopaguropsis atlantica* Wass, 1963, and evidence from larval characters of some generic relationships within the Paguridae. *Bulletin of Marine Science, Coral Gables* **21** 1: 237–255.

—— **& Rice, A. L.** 1964. Juvenile morphology and the development of taxonomic characters in *Paguristes sericeus* A. Milne-Edwards (Decapoda, Diogenidae). *Crustaceana, International Journal of Crustacean Research, Leiden* **10** (1): 53–69.

Quintata, R. & Konishi, K. 1986. On the prezoeal stage: observations on three *Pagurus* species (Decapoda, Anomura). *Journal of Natural History, London* **20:** 837–844.

Rice, A. L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyra. *Transactions of the Zoological Society of London* **35**: 271–424.

—— **& Provenzano, A. J.** 1965. The zoeal stages and the glaucothoe of *Paguristes sericeus* A. Milne-Edwards (Anomura, Diogenidae), *Crustaceana, International Journal of Crustacean Research, Leiden* **8** 3: 239–254.

Samuelsen, T. J. 1972. Larvae of *Pagurus variabilis* Milne-Edwards & Bouvier (Decapoda, Anomura) reared in the laboratory. *Sarsia, Universitetet i Bergen* **48**: 1–12.

Sars, G. O. 1890. Bidrag til kundskaben om Decapodernes Forvandlinger, II Lithodes-Eupagurus-Spiropagurus-Galathodes-Galathea-Munida-Porcellana-(Nephrops). *Archiv for Mathematik og Naturvidenskab, Oslo* **13**: 133–201.

Steedman, H. F. 1976. *Part V. General and applied data on formaldehyde fixation and preservation of marine zooplankton pp. 103–154.* In: Steedman, H. F. Monographs on oceanographic methodology. Zooplankton fixation and preservation. The Unesco Press, Paris, 354 pp.

Tirmizi, N. M. & Siddiqui, F. A. 1980. Notes on the laboratory reared larvae of *Pagurus kulkarnii* Sankolli (Decapoda, Paguridae). *Crustaceana, International Journal of Crustacean Research, Leiden* **38** (2): 155–168.

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